

# THE ICHNOGENUS *BEACONITES* AND ITS DISTINCTION FROM *ANCORICHNUS* AND *TAENIDIUM*

by D. G. KEIGHLEY and R. K. PICKERILL

**ABSTRACT.** *Beaconites* is a trace-fossil name that has been adopted indiscriminantly for unlined, lined, unwalled, thinly walled, and thickly walled, meniscate backfilled burrows. The confusion is further exacerbated by the inconsistent use of the terms 'wall' and 'lining'. A wall and a lining (a type of wall) are herein restricted to features actively constructed by the burrower, and are considered distinct from peripheral features produced by simple excavation or during locomotion. Differences in the type of meniscate backfilling are also recognized, and may assist in the distinction of ichnotaxa. *Beaconites*, and likewise the type ichnospecies *B. antarcticus*, is a lined (walled) meniscate trace fossil; *B. barretti*, the ichnospecies most popularly assigned to the ichnotaxon, is actually unlined and unwalled, and cannot therefore be included within *Beaconites*. Recent emendments to *Taenidium* describe it essentially as an unlined meniscate backfilled burrow. The diagnosis of *Taenidium* is, however, further emended to clarify that it is an unwalled structure. Forms previously assigned to *B. barretti* can therefore be included within *Taenidium* as *T. barretti*. Emendments to the original diagnosis of *Ancorichnus* describe this trace fossil as a walled ichnotaxon. These emendments are rejected because this would place the ichnogenus in junior synonymy with *Beaconites*; instead, the original diagnosis of *Ancorichnus* is re-established. Two ichnospecies, *A. capronus* and *A. coronus* are, nevertheless, considered to be separate ichnospecies of *Beaconites*, namely *B. capronus* and *B. coronus*. The type ichnospecies, *A. ancorichnus*, is distinguished by a structured mantle peripheral to a meniscate core. The mantle is not considered as a wall structure since it is formed by the locomotive behaviour of the burrow producer.

SEVERAL authors have commented upon the ichnotaxonomic problems associated with meniscate trace fossils. For example, Frey *et al.* (1984) discussed *Ancorichnus* Heinberg, 1974, and *Scoyenia* White, 1929; D'Alessandro and Bromley (1987) discussed both *Mnensteria* Sternberg, 1833, and *Taenidium* Heer, 1877. These authors, with, for example, Squires and Advocate (1984), O'Sullivan *et al.* (1986), Brück (1987) and Gordon (1988) also suggested that further synonyms may exist for these and other meniscate trace fossils, including *Beaconites* Vialov, 1962.

One of the major problems with addressing the potential synonymies of *Beaconites* is the nature of this ichnotaxon's margins, its internal structure and, to a lesser extent, its overall size and orientation. Such diagnostic criteria ('ichnotaxobases'; Bromley 1990) have been confused and applied indiscriminately within *Beaconites*. Accordingly, *Beaconites* has been variably described as a small, walled meniscate burrow (Vialov 1962), a large walled meniscate burrow (Häntzschel 1975), a smoothly-lined meniscate burrow (Bradshaw 1981), an unlined meniscate burrow (Frey *et al.* 1984; Squires and Advocate 1984; Brück *et al.* 1985), and a weakly or unwalled meniscate burrow (D'Alessandro and Bromley 1987).

Since many of the terms employed in distinguishing *Beaconites* and related ichnotaxa have thus been used with different or occasionally (and more problematically) unspecified meanings, the terminology adopted for this contribution is initially summarized. The diagnostic criteria of *Beaconites* are then re-examined, particularly regarding its distinction from the morphologically similar ichnotaxa *Ancorichnus* and *Taenidium*. This is followed by revised synonymy listings for *Ancorichnus*, *Beaconites*, and *Taenidium*.

## TERMINOLOGY

*Backfill structure (backfilled burrow)*

Bioturbation in softgrounds caused by the active redeposition of sediment (active fill) immediately behind a burrowing animal. Essentially, it is produced by the axial migration of a burrow that itself is not preserved (Bromley 1990). In contrast, an *open burrow* is occupied and maintained by an animal and passively (or occasionally actively) filled later (Bromley 1990, p. 266). Backfilling probably assists in the organism's forward movement (Chamberlain 1971a; Heinberg 1974) and the transport of such material to the rear of the producer may occur either externally, around the burrower, or internally through the digestive tract. The backfill may therefore contain both faecal and nonfaecal components.

*Boundary*

The sharp or diffuse interface between the host sediment and the bioturbation structure. In contrast, the *outline* or *margin* (herein used interchangeably) are more general terms describing the outermost part of the trace fossil and may include the boundary, wall, mantle, some other peripheral structure, or a combination of these structures.

*Branching*

Four types of branching (*sensu lato*) have been recognized (D'Alessandro and Bromley 1987). Of these, 'false' and 'secondary successive' branching are applied to trace fossils that only apparently ramify and are not truly branched.

*Wall*

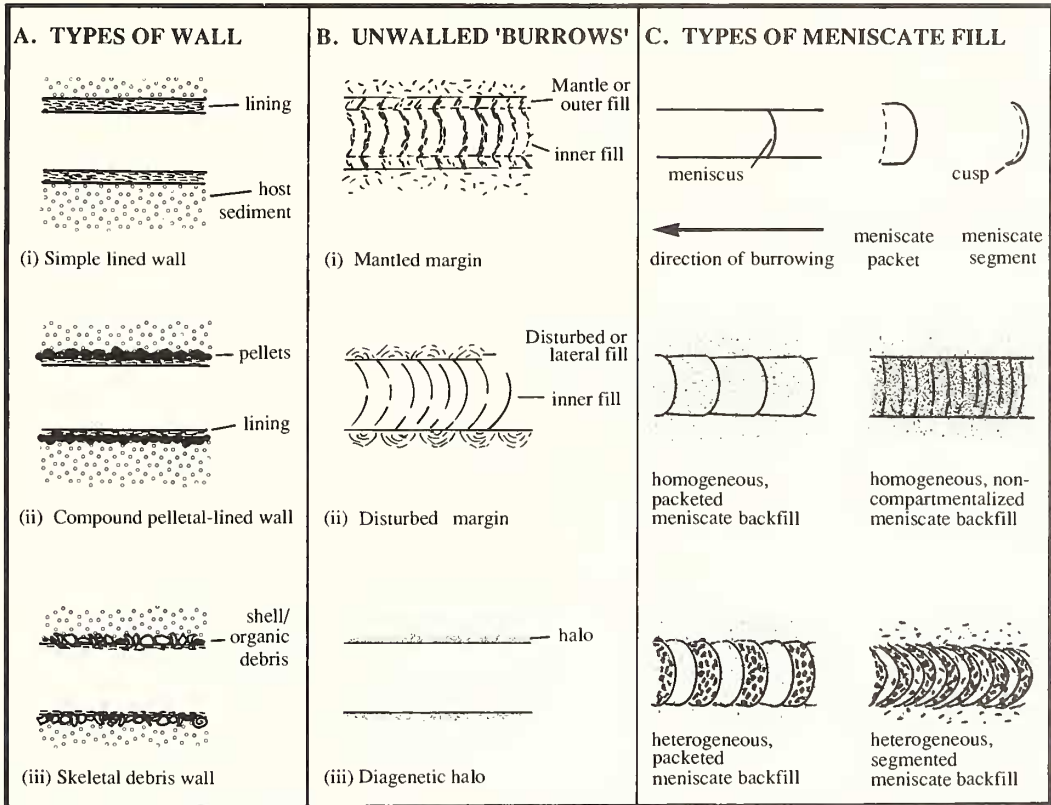
A feature actively constructed by a burrowing organism to help provide the animal with temporary or permanent protection from the external environment. In more permanent dwelling burrows the wall might seal off permeability, allow canalization of the irrigation stream (Schäfer 1956) or prevent burrow collapse. In backfilled structures the need for a constructional wall is of little importance, since the 'burrow' is not permanent and is immediately closed off behind the producer. Note that the simple excavated boundary of a burrow is not a wall in the true sense because there has been no active construction, only excavation. A true wall may be simple or complex, thin or thick, and may be composed of compacted sediment, a sediment lining, pelletal, faecal, skeletal or vegetational material, or a combination of such (Text-fig. 1A–B).

*Lining*

A type of wall structure formed by the active or passive attachment of typically fine-grained material to mucus, applied by the producer to the interior side of its burrow. It is observed as the inner part of a complex wall or, alternatively, as the only wall structure produced (Text-fig. 1A, and Bromley 1990, p. 20, fig. 2.7). A lining in a backfilled structure would probably only be actively produced as a by-product of selective sediment sorting by the burrower (Clifton and Thompson 1978), or passively accumulated on mucus secreted locally to assist passage of a soft-bodied organism through the substrate.

*Mantle*

The outer zone of a two-zoned burrow fill (Text-fig. 1B). Heinberg (1974, p. 10) explained that this feature is formed by a burrowing organism's hydrostatic anchor for the purpose of forward locomotion. Mantles are not constructed as insulation against external conditions or to ease passage through the substrate, but are actual locomotory evidence of such passage. Therefore, as pointed



TEXT-FIG. 1. Morphological features of burrows. A, various types of wall construction (note that a lining is a type of wall). B, various types of unwallled burrow margins; (i) and (ii) are backfilled structures and hence not 'burrows' in the strictest sense; (iii) is a simple excavated burrow; no construction has occurred at the burrow boundary and so it is classed as being 'unwallled'. C, styles of meniscate backfill.

out by Heinberg (1970) and reiterated by Bromley (1990, p. 149), the mantle is 'conceptually distinct from a true burrow wall'.

### *Meniscus*

This term is utilized in a more restrictive sense than its Greek derivation of 'shaped like a crescent moon', being limited to a transversely-oriented, arcuate to almost chevron-shaped, internal interface that is observed on a surface trail in plan view, or in axial cross-section in a burrow or backfilled structure. In this definition, use of the term 'internal interface' emphasizes the two-dimensional nature of a meniscus. It has no longitudinal dimension (i.e. it appears as a thin line running transversely across the structure). The concave side marks the direction in which the producer is travelling (Text-fig. 1c). The meniscus is produced by the termination of an episode of material backfilling behind the burrower.

Between successive menisci, the amount of backfilling that can occur is variable (Text-fig. 1c). If the amount of material processed is large, a bullet-shaped compartment, or *meniscate packet*, of material is produced. With less material present between successive menisci, a three-dimensional, dish-shaped compartment forms. In cross-sectional view, menisci converge at the margin of the structure forming cusps, and the general appearance is that of a crescent (*meniscate segment*). A third style of meniscate backfill comprises a *non-compartmentalized meniscate backfill*, where

menisci are too densely, or diffusely, stacked for separate segments or packets to be recognized. A packet is most likely the result of a single excretory event (whether the packet contains visible organic waste in the form of pelleted aggregates, or not), whereas non-compartmentalized backfill may represent more continuous external backfilling (with or without scattered, intermixed, faecal pellets). Potentially, the three types of meniscate fill are part of an intergradational sequence dependent on how much material is processed, stuffed or excreted, and compacted behind the animal as backfill at any one time between periods of forward locomotion. Meniscate backfill may be *homogeneous* whereby the backfill (compartmentalized or not) is essentially of the same uniform composition (sediment or faecal) throughout the structure. Alternatively, the backfill may be *heterogeneous*, whereby more than one type/grain-size of internally or externally processed sediment (and/or faecal material) is present or was presumed originally to be present before being weathered out. Physical transport outside the body of the animal may itself provide for alternating meniscate composition by way of the physical or compositional sorting of the sediment by the organism (D'Alessandro and Bromley 1987; Pickerill 1989).

#### DIAGNOSTIC CRITERIA OF *BEACONITES*

The nature of the margin in a burrow or backfill structure, together with the presence or absence of branching, are the significant primary diagnostic criteria at the ichnogenic rank for the distinction of most meniscate trace fossils, as emphasized by D'Alessandro and Bromley (1987), D'Alessandro *et al.* (1987) and Bromley (1990). Factors such as lithology or geographical distribution should not be considered as criteria for identifying *Beaconites* or any other ichnotaxon, because they are contrary to the concept of ichnotaxobases (Pemberton and Frey 1982; Bromley 1990; Pickerill 1994). The following discussion concentrates on the true nature of the burrow outline in *Beaconites*, and attempts to clarify problems in the diagnosis and differentiation of morphologically similar ichnogenera, particularly *Taenidium* and *Ancorichnus*.

##### *Beaconites as a walled meniscate trace fossil*

Although based solely on photographs rather than specimens or field observations, *Beaconites* was validly erected by Vialov (1962, p. 727). In the preamble to his diagnosis, he stated that the walls were 'fine' and 'clearly distinguishable'. Although Vialov's definition of a 'wall' was not provided, his comments are best interpreted as meaning an actively constructed wall comprised of fine-grained material, or a tubular lining, as the terms are utilized herein. Bradshaw (1981, p. 630), in emending the ichnogenic diagnosis, similarly noted that the ichnotaxon was distinguishable as 'tubular burrows' with a smooth burrow lining. This same construction, occurring as a sand lining, was also noted in her emended diagnosis of the type ichnospecies *B. antarcticus* Vialov, 1962. Such characteristics have also been used consistently by other workers (e.g. Webby 1968; O'Sullivan *et al.* 1986; Woolfe 1990; Sarkar and Chaudhuri 1992) in their interpretation of *Beaconites*. The presence of a lined wall is therefore a primary diagnostic criterion for the definition of this trace fossil.

Despite Vialov's (1962) original diagnosis and Bradshaw's (1981) emendment, several subsequent authors (e.g. Frey *et al.* 1984; Squires and Advocate 1984) considered the ichnogenus to be unlined or unwalled. Accordingly, they suggested that *Beaconites* might be a junior synonym of some other unwalled meniscate burrow. D'Alessandro and Bromley (1987, p. 751) also initially considered the ichnotaxon as dubious, '...having a weak wall or none at all, and it should probably be included in *Taenidium*'. In contrast, they later commented that *B. antarcticus* seemed to have a wall, and that details of the burrow boundary, from photographs, topotypic material, and descriptions, were unclear (D'Alessandro and Bromley 1987, p. 757). Examination of unweathered material was therefore considered to be necessary before the relationship between *Beaconites* and *Ancorichnus* or *Taenidium* could be clarified. It is, however, difficult to visualize how examination of unweathered specimens would alleviate nomenclatural difficulties since, if Bradshaw's (1981) specimens are



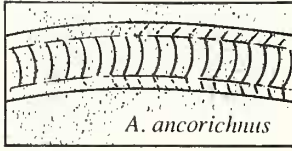
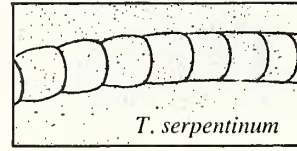
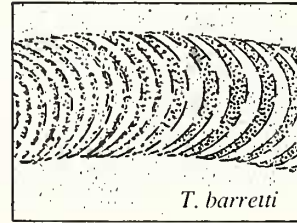
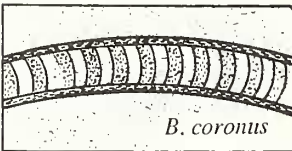
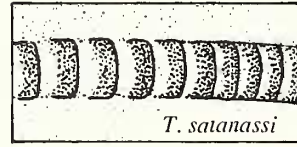
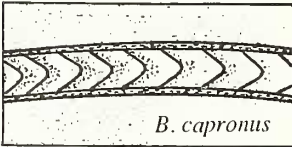
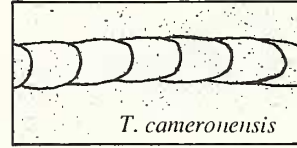
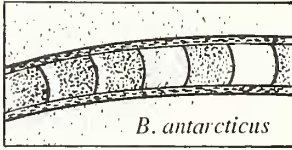
considered to be too badly weathered, and Vialov's (1962) material was never collected, it cannot be ascertained what type of marginal structure constituted the original *Beaconites* (and assignment of new material would depend on the diagnoses of the original ichnotaxa). As with many ichnotaxa proposed in the nineteenth century, ichnologists have only the original diagnosis and illustrations to work with. From both the validly introduced original and emended diagnoses, *Beaconites* must remain a walled meniscate burrow.

The confusion over whether *Beaconites* was a walled or unwalled burrow probably persisted not only due to poorly defined terminology but also because of inclusion within it of large meniscate forms. Gevers *et al.* (1971) were the first to consider large meniscate burrows as *B. antarcticus*, possibly on the mistaken belief that Vialov's (1962) specimens could attain a diameter of 150 mm. In comparing their giant forms with other large burrows, they noted (Gevers *et al.* 1971, p. 83) that their largest examples 'compare in dimensions with the largest (150 mm) of *B. antarcticus* as described by Vialov'. The largest specimens described by Vialov (1962) were, however, no larger than 15 mm in diameter. Gevers *et al.* (1971) also suggested that nomenclatural distinction from Vialov's (1962) specimens might be justified at the ichnospecific level, but that this distinction should be based upon significant differences in both the thickness of the meniscate packets, and in the 'septal' (meniscate) shape. One of the differences they failed to recognize, however, was the contrast in the outline of the trace fossil between their material and the type specimen of *B. antarcticus*. They interpreted the coalescing 'ridges' (individual meniscate segments) at the margin as a lining, or 'welt', that they considered to be the erosional remnants of 'outer consolidated tubes'. The 'welts' were noted to thicken where the burrow curved sharply and the 'septal' ridges were close together. Photographs of these large forms, which they noted as containing a marginal furrow, similarly illustrate the burrow outline being formed by the merging of transverse meniscate ridges that were produced by backfill (Gevers *et al.* 1971, pl. 18, figs 1, 2, 4). The large forms apparently had no true lining or other type of wall structure. In comparison, their small burrows had a distinct lining and hence were walled (Gevers *et al.* 1971, pl. 18, fig. 3) and correctly described as *B. antarcticus*.

Recognizing that two distinct morphologies were being included within the same ichnospecies, Bradshaw (1981) followed the suggestion of Gevers *et al.* (1971) and introduced a second ichnospecies of *Beaconites*. The description (= diagnosis) of *B. barretti* Bradshaw, 1981 (p. 631) stated that the sediment compartments '... may merge laterally to form a crude burrow lining...' when the meniscate segments '... meet the burrow wall at an acute angle'. However, in her specimens, the 'lining' of *B. barretti* is produced by the backfill, specifically the peripheral margins of the meniscate segments. The producer simply excavated and backfilled its burrow. No wall was constructed. Neither is the presence of a true wall lining, or any other sort of wall structure, supported by her illustrations (Bradshaw 1981, figs 17 and 18). *B. barretti*, both as defined and illustrated, is not walled. Indeed, of all the large meniscate trace fossils previously or subsequently described and figured as *B. antarcticus*, *B. barretti*, or simply *Beaconites* (e.g. Gevers *et al.* 1971; Häntzschel 1975; Pollard 1976; Allen and Williams 1981a, 1981b; Bradshaw 1981; Graham and Pollard 1982; Narbonne 1984; Eagar *et al.* 1985; Brück 1987; Dam and Andreasen 1990; Woolfe 1990; Pearson 1992; Tegan and Curran 1992), none appears either lined or walled. This clearly contrasts with both the original and emended diagnosis of the ichnogenus. These large backfilled burrows cannot be included within *Beaconites* and must, instead, be incorporated within an alternative meniscate ichnotaxon, or re-introduced as a new ichnogenus. The former option is adopted for the reasons discussed below.

#### *Unwalled meniscate trace fossils: large 'Beaconites' forms and Taenidium*

To determine to which ichnotaxon the large '*Beaconites*' forms should be assigned, it is necessary to review briefly the current status of simple, unwalled, backfilled burrows. Debate has been going on since the mid-nineteenth century as to the potential synonymies of the meniscate trace fossils *Muensteria*, *Keckia* Glocker, 1841, *Taenidium*, and *Beaconites* (e.g. Fischer-Ooster 1858; Heer 1877;

*Ancorichnus**Taenidium**Beaconites*

TEXT-FIG. 2. Currently accepted ichnospecies of *Ancorichnus*, *Beaconites*, and *Taenidium*, showing the variation that might occur in backfill morphology for each ichnospecies.

Schröter 1894; Liburnau 1900; Wilckens 1947; Frey *et al.* 1984; Squires and Advocate 1984; O'Sullivan *et al.* 1986; McCann and Pickerill 1988). Of most importance, D'Alessandro and Bromley (1987, p. 747) considered *Muensteria* a name unavailable for trace fossils, concluding that '... on the basis of its first ichnospecies *Taenidium* is available for the unbranched ichnospecies of *Muensteria*...' Branched, annulate burrows of *Taenidium* were transferred to *Cladichnus* D'Alessandro and Bromley, 1987.

Several of the actions of D'Alessandro and Bromley (1987) are, however, in need of clarification. As Sternberg's (1833) original *Mueuseria* included algae, coprolites and possible specimens of *Chondrites* Sternberg, 1833, it was therefore erected as a heterogeneous ichnogenus, and thus invalidly introduced. It would, however, remain as an available name (International Code of Zoological Nomenclature 1985, Articles 10–14, and 17). Although the heterogeneous nature of *Mueuseria* was addressed in the emendments of Fischer-Ooster (1858), many of his actions, particularly with regards to the introduction of three 'subgenera', were again probably invalid as dictated by today's I.C.Z.N. D'Alessandro and Bromley (1987) considered *Taenidium* as an unbranched ichnotaxon because the type ichnospecies was diagnosed as unbranched. This is not the case because Heer (1877) did not consider branching as an important diagnostic criterion. The original diagnosis of the ichnogenus (as opposed to that of the type ichnospecies) clearly stated that the taxon was '*rarius ramosa*' (rarely branching) in the sense that one or two ichnospecies, such as *T. fischeri* Heer, 1877, could branch. Additionally, according to Heer (1877), Wilckens (1947), and McCann and Pickerill (1988), amongst others, *Taenidium* was differentiated from forms ascribed to *Mueuseria* because the latter may lack packeting and a ringed, or annulate, boundary and instead, contain only simple, non-compartmentalized meniscate ('runzelig quergestreift' (transversely

TRACE FOSSIL	AUTHORS	Recorded burrow widths (mm)				
		0	50	100	150	200
<i>Taenidium</i> '	Smith <i>et al.</i> 1993	■ (8-15 mm).				
<i>Taenidium</i> '	D' Alessandro <i>et al.</i> 1993	■ (12-25 mm).				
<i>T. serpentinum</i>	Chamberlain 1977	■ (1-2 mm).				
<i>T. serpentinum</i>	Dam 1990a	■ (5-10 mm).				
<i>T. satanassi</i>	D' Alessandro and Bromley 1987	■ (4-14 mm).				
<i>T. cameronensis</i>	Brady 1947	■ (12-18 mm).				
<i>T. barretti</i>	Gevers <i>et al.</i> 1971	■ (27-103 mm).				
<i>T. barretti</i>	Ridgway 1974	■ (11-110 mm).				
<i>T. barretti</i>	Allen and Williams 1981	■ (30-250 mm).				
<i>T. barretti</i>	Bradshaw 1981	■ (30-150 mm).				
<i>T. barretti</i>	Graham and Pollard 1982	■ (35-125 mm).				
<i>T. barretti</i>	Brück 1987	■ (150-230 mm).				
<i>T. barretti</i>	This study	■ (5-51 + 75 mm).				

TEXT-FIG. 3. Recorded widths of *Taenidium* and its ichnospecies from selected literature. As these are not necessarily diameters, the data may contain some positive skew (Graham and Pollard 1982). In addition to the 75 mm wide specimen from the Port Hood Formation (Plate 1, figs 5-6), this study also measured a total of 56 specimens from the Perry Formation (see also Plate 1, figs 2-4). Over a discontinuous area of the same bed (approximately 6 m by 2 m), burrows range in width from 5 to 51 mm (mean = 18.1 mm, standard deviation = 9.7).

striped); Wilckens 1947) backfill. The emended diagnosis of *Taenidium* (D'Alessandro and Bromley 1987) similarly stated that these burrows should contain a segmented fill articulated by meniscus-shaped partings (i.e. the backfill is distinctly compartmentalized, consistent with the diagnoses of Heer 1877 and Wilckens 1947). Contrary to this, from D'Alessandro and Bromley's (1987, p. 747) sweeping statement quoted above, and their discussion of other potentially synonymous ichnotaxa, it would appear that all unbranched forms of *Muensteria*, and other meniscate ichnotaxa, are to be included within *Taenidium*, regardless of the style of backfill. This might be seen as an excessive lumping of ichnotaxa but, as discussed earlier, segments and simple backfill in particular may potentially intergrade within a single burrow. Differentiation of separate ichnogenera for variations in the style of backfill may therefore be considered inappropriate.

Despite the problems outlined above, to promote ichnotaxonomic stability we follow D'Alessandro and Bromley (1987) and include all radially branched, and potentially palmate, ichnospecies of both *Muensteria* and *Taenidium* within *Cladichnus*. Similarly we follow their suggestion to include unbranched ichnospecies of *Muensteria* within *Taenidium* (note that different specimens may cross each other giving a falsely branching appearance, Plate 1, fig. 1). Variation in the type of backfill contained within these, and other potentially synonymous, unbranched, meniscate burrows is therefore relegated to an ichnospecies-level taxobase.

Another emendment to the diagnosis of *Taenidium* proposed by D'Alessandro and Bromley (1987) is, however, still required. These authors potentially allowed for both unlined and thinly lined burrows to be included within the ichnogenus. From their diagnosis, the production of a thin, continuous lining can be considered a morphological feature comparable to no lining being present, and not worthy of ichnogenetic distinction. The production of a thick lining, in contrast, is inferred to be a morphological feature different from that of a thin lining and significant enough to warrant a separate ichnogenetic name. What is construed as 'thin', or for that matter 'thick', is arbitrary, and such a division cannot improve ichnotaxonomic stability. The presence of any form of continuous burrow lining, thick or thin, should be considered a morphologically similar criterion, and different to that of no lining. The presence or absence of a continuously lined wall is therefore an important ichnotaxobase. Consequently, as a further emendment to the diagnosis of *Taenidium*,



we propose that this ichnogenus should be restricted to unwalled, and thus unlined, burrows. Such an emendment would also reinforce the differences between *Beacouites* and *Taenidium*, as discussed in the previous section, and avoid further lumping of ichnotaxa.

Accordingly, although D'Alessandro and Bromley (1987) concluded that *Beacouites* should probably be included within *Taenidium*, only *B. barretti* is regarded as synonymous. Without exception, *B. barretti* burrows are unbranched, meniscate, cylindrical and, above all, unlined. Such burrows are distinguished as a distinctive ichnospecies, specifically *T. barretti* (Bradshaw), on the basis of the heterogeneous, thinly segmented or non-compartmentalized, arcuate meniscate fill. The style of meniscate fill in these burrows is clearly at variance with the three ichnospecies of *Taenidium* considered by D'Alessandro and Bromley (1987), all of which are distinctly packeted (Text-fig. 2) but this is a legacy of the latter authors' relegation of style of meniscate fill to an ichnospecies-level diagnostic criterion.

The size of a burrow has, in the past, been used as a significant criterion in formulating new ichnogenera (e.g. *Megagyrolithes* Gaillard, 1980) as well as a secondary criterion in distinguishing ichnospecies within an ichnogenus (e.g. *Helminthopsis* Heer, 1877). The range of widths measured for specimens of *T. barretti*, although typically much greater, overlap to some degree those widths previously measured in other ichnospecies of *Taenidium* and *Muensteria* (Text-fig. 3). Therefore, despite the measured widths of *T. barretti* probably including some positive skew, resulting from the measurement of widths on bedding planes as opposed to true burrow diameters (Graham and Pollard 1982), it would be unwise for these burrows to be considered distinct at the ichnogenic level based on size. *T. barretti* observed at various localities in eastern Canada further illustrate the variability in size that can be encountered within otherwise morphologically similar specimens (Plate 1).

#### *Vertical escape and vertical adjustment structures*

Whether typically large, vertically oriented trace fossils containing distinctive arcuate, concave upwards, nested menisci should be attributed to a previously established meniscate backfilled burrow, such as *Beacouites*, was questioned by Bridge *et al.* (1986). Most commonly, such trace fossils have been left in open nomenclature and described simply as 'escape structures' or 'equilibrium structures' (e.g. Eagar *et al.* 1985; Sarkar and Chaudhuri 1992). Occasionally vertical 'burrows' have been erroneously named as *Beacouites*: the structures of Bridge and Gordon (1985), Bridge and Droser (1985), and Berg (1977) do not contain a wall, whereas those of Allen and Williams (1981a, 1981b) and Brück *et al.* (1985) additionally do not have an observable meniscate structure.

The morphological characteristics of a trace fossil provide the only feasible diagnostic criteria for distinguishing ichnotaxa. The behavioural interpretation of a trace fossil is not a valid criterion, though morphological features may be indicative of one particular behaviour, or a variety of behaviours: meniscate backfill containing faecal matter or meniscate packeting is typical of

---

#### EXPLANATION OF PLATE I

Figs 1–6. *Taenidium barretti* (Bradshaw). Burrows of variable size and variable distinctiveness of meniscate fill; 1–4, preserved in convex epirelief; 5–7, preserved in convex hyporelief; they are ubiquitously non-compartmentalized and meniscate and much less distinct where burrow-fill is of uniform composition. 1, Alma, southeast New Brunswick, Canada; alluvial fan deposits, Hopewell Conglomerate, Lower Carboniferous;  $\times 0.6$ . 2–4, McCann Cove, southwest New Brunswick, Canada; partly calcified alluvial fan deposits, Perry Formation, Devonian; 2,  $\times 0.4$ ; 3,  $\times 0.5$ ; 4,  $\times 0.9$ . 5, near Port Hood, Cape Breton Island, Nova Scotia, Canada; fluvial bar sandstones, upper Port Hood Formation, Upper Carboniferous;  $\times 0.2$ . 6, oblique view of same specimen as in fig. 5. All field photographs, specimens not collectable.







fodinichnia (Bromley 1990), but backfilled burrows lacking distinct faecal content or meniscate packeting may represent repichnia, equilibrichnia of Bromley (1990), or even fugichnia. Vertically-upward oriented, non-compartmentalized, meniscate structures may be repichnia, while oblique, lateral or vertically downward-oriented structures may represent adjustment or escape from lower water tables, desiccation, erosion or predation (cf. Sarkar and Chaudhuri 1992, fig. 5; if way-up was not known, how would the two structures be differentiated?). Since *Taenidium* has never been restricted to a particular orientation with respect to stratification, simple, vertically-upward oriented, backfilled structures with arcuate menisci can be accommodated within this ichnogenus. Vertically oriented 'escape' structures that contain irregularly patterned, downward-deflected backfill (e.g. Pieńkowski 1985, plate 1B; Bromley 1990, fig. 5.8e; Gierlowski-Kordeck 1991, fig. 7) are distinguishable from *Taenidium* and must, for the present, be retained in open nomenclature.

#### *Beaconites and other walled meniscate trace fossils*

Since *Beaconites* has a distinct wall structure, the relationship with other supposedly walled meniscate trace fossils, particularly *Scoyenia* and *Ancorichnus*, must also be considered. *Scoyenia*, originally described in botanical terms, has subsequently been considered a walled, meniscate burrow that possesses longitudinally striated linings (Frey *et al.* 1984). In this sense *Scoyenia* and *Beaconites* are potential taphonomic variants of the same burrow, taxonomic classification depending on the presence or absence of such longitudinal striations. Bromley (pers. comm. 1993) suggested that *Scoyenia* is actually unlined and unwalled, with striations produced on the simple excavated margin of a transient burrow. If this is the case, it would mean that *Scoyenia* and *Taenidium* are potential taphonomic variants. The separate identity of *Scoyenia* is, however, retained for ichnotaxonomic stability.

When originally proposed, *Ancorichnus* was monospecific. The type, *A. ancorichnus* Heinberg, 1974, was described as an undulating 'cylindrical meniscus filled tunnel with a distinct mantle'. The mantle was considered as the outer part of a two-zoned burrow fill and had, as an internal structure or ornament, a distinct orientation of mica grains. The mantle, with its internal ornamentation, was not believed to have been formed by the construction of a wall but rather by the burrowing organism's hydrostatic anchor for the purpose of forward locomotion (Heinberg 1974, p. 10). As noted by Bromley (1990, p. 149), this type of margin is 'conceptually distinct from a true burrow wall'.

Heinberg (1974, p. 9) also recognized that, in some cases, the mantle could be weathered out and, instead, be represented as a groove on each side of the meniscate core-fill. In such cases, the mantle might be mistaken for a weathered-out wall. Since no internal ornament would be preserved in the grooves, there would be essentially no difference between *Ancorichnus* and those burrows described by Vialov (1962) or Bradshaw (1981) as *Beaconites*. Depending upon taphonomic variability, problems may therefore also exist in the distinction of *Ancorichnus* and *Beaconites*. Nevertheless, the presence or absence of an oblique or transverse internal fabric in the marginal structure of a meniscate trace fossil will best determine whether it has a mantle or a lining and whether it should therefore be assigned to *Ancorichnus* or *Beaconites*.

Further ichnotaxonomic problems have arisen because of the proposed changes to *Ancorichnus* by Frey *et al.* (1984, p. 514). Linings, mantles and walls became less rigidly defined in their emended diagnosis: '...relatively thick, unornamented wall linings surrounding well-developed, meniscate burrow fills. Distal ends of menisci may blend directly into the wall structure.' Essentially, the mantle in *A. ancorichnus* was considered as a wall or a wall lining, and its internal structure was relegated to a feature of ichnospecific significance. Accordingly, *A. capronus* Howard and Frey, 1984, and *A. coronus* Frey *et al.*, 1984, two simply lined burrows, were also accommodated within the ichnogenus, even though they did not have a distinctly structured mantle.

Although Frey *et al.* (1984) made careful comparisons with several other meniscate burrows with which *Ancorichnus* and *Scoyenia* could be confused, synonymy with *Beaconites* was dismissed because they considered *Beaconites* an unlined burrow (Frey *et al.* 1984, p. 517). However, as

*Beaconites* is lined, acceptance of the emended diagnosis of *Ancorichnus* by Frey *et al.* (1984) would mean that there is no primary criterion to distinguish it from *Beaconites*, and it would therefore become a junior synonym. By rejecting the emendment of Frey *et al.* (1984) in favour of the more precise description originally provided by Heinberg (1974), the important distinguishing characteristic of *Ancorichnus* is retained, namely the presence of a distinctly structured mantle. It is morphologically and behaviourally distinct, because the burrow outline is produced by a method akin to active backfill; in *Beaconites* the outline is a constructional lining. *Ancorichnus* remains monospecific, containing only *A. ancorichnus*. D'Alessandro *et al.* (1993) suggested that *A. coronus* may not have a discrete wall structure, but rather that its marginal structure was formed by partial overlapping of contiguous menisci (as is the case with *B. barretti*). They suggested placing the ichnospecies within *Taenidium*. If this were done, *A. coronus* would be a junior synonym of *T. barretti*, as revised herein. However, the original diagnosis of the ichnospecies is followed by Frey *et al.* (1984), and *A. coronus* is considered to be walled. Even so, it could then be considered a junior synonym of *B. antarcticus* because of its distinct, unstructured wall lining. This contribution proposes that the ichnospecific identity of *A. coronus* be retained, albeit within the walled ichnogenus *Beaconites*. As with *Taenidium*, variations in fabrication of meniscate fill can be used to differentiate ichnospecies. Meniscate packets of a thickness approximately equivalent to the diameter of the burrow typify *B. antarcticus*, whereas most specimens of what have previously been called *A. coronus* have regularly arranged, heterogeneous, longitudinally short meniscate packets or even segments (Text-fig. 2). The latter forms are therefore identified separately as *B. coronus* (Frey *et al.* 1984). *A. capromus*, by way of its distinctive chevron pattern of meniscate infill within a thin, unstructured wall lining, is similarly retained as a distinct ichnofossil, becoming *B. capromus* (Howard and Frey, 1984).

#### SYSTEMATIC PALAEOLOGY

As this contribution deals primarily with the clarification of *Beaconites*, and its relationship to the morphologically similar *Ancorichnus* and *Taenidium*, included synonymy is restricted to these three ichnotaxa. Only a brief systematic treatment of *Taenidium* was provided by D'Alessandro and Bromley (1987), and we have now expanded and updated their listing. In numerous cases, ichnotaxa have only been illustrated schematically (in varying degrees of detail) and with limited accompanying description. Such references can only be considered as uncertain synonymies (and are prefixed '?') and typically are only identified to the ichnogenetic level. Additionally, since *Taenidium* is now considered to be the first valid name for specimens of *Muensteria*, former ichnospecies of the latter that are now of indeterminate ichnospecific designation within *Taenidium*, or are reassigned to other ichnotaxa, are included within the ichnogenetic synonymy of *Taenidium*.

#### Ichnogenus ANCORICHNUS Heinberg, 1974

- non* 1984 *Ancorichnus capromus* Howard and Frey, p. 201, figs 2–3 [= *Beaconites capromus*].
- non* 1984 *Ancorichnus capromus* Howard and Frey; Frey *et al.*, p. 514 [= *Beaconites capromus*].
- non* 1984 *Ancorichnus coronus* Frey *et al.*, p. 511, figs 1D [copy of Stanley and Fagerstrom 1974, fig. 6], 1E, 3A–C [= *Beaconites coronus*].
- non* 1985 *Ancorichnus capromus* Howard and Frey; Frey and Howard, p. 373, figs 5.6, 5.8, 16.3D [= *Beaconites capromus*].
- non* 1985 *Ancorichnus capromus* Howard and Frey; Frey and Howard, p. 122, fig. 2 [copy of Howard and Frey 1984, fig. 2; = *Beaconites capromus*].
- non* 1985 *Ancorichnus capromus* Howard and Frey; Frey and Pemberton, p. 90, fig. 26 [copy of Howard and Frey 1984, fig. 2; = *Beaconites capromus*].
- ?1986 *Ancorichnus* isp.; Valenzuela *et al.*, p. 129.
- non* 1987 cf. *Ancorichnus coronus* Frey *et al.*; D'Alessandro *et al.*, p. 285, fig. 2 [?= *Taenidium barretti*].
- non* 1989 *Ancorichnus capromus* Howard and Frey; Martino, p. 393, fig. 5.5 [= *Beaconites capromus*].
- non* 1990 *Ancorichnus capromus* Howard and Frey; Frey, p. 204, fig. 7D [= *Beaconites capromus*].

LOCATIONS *authors	AGE	ENVIRONMENT									
		Alluvial Fan	Lacustrine	Floodplain /Overbank	Crevasse Splay /Levé	Fluvial	Distributary Channel	Mouth Bar /Intertidal	Inner Shelf (a.s.w.b.)	Outer Shelf (b.s.w.b.)	Submarine fan /Abyssal
Nebraska, USA <sup>1,2</sup>	Miocene	■■■■■				■■■■■					
S England <sup>3</sup>	Oligocene						■■■■■				
Utah, USA <sup>4,13</sup>	Eocene							~~~~~			
Alberta, Canada <sup>14</sup>	Cretaceous							■■■■■			
Jameson Land, Greenland <sup>15-16</sup>	Jurassic							+++++			
Milne Land, Greenland <sup>17,18</sup>	Jurassic							+++++			
West Virginia, USA <sup>19</sup>	Carboniferous							~~~~~			
S Victoria Land Antarctica <sup>20-24</sup>	Devonian	■■■■■	■■■■■			■■■■■					

KEY: ++++ *A. ancorichnus* ■■■■■ *B. antarcticus* ~~~~~ *B. capronus* ■■■■■ *B. coronus*

TEXT-FIG. 4. Temporal and environmental distribution of ichnospecies of *Ancorichnus* and *Beaconites*. Only references to confidently assigned ichnospecies and of known environment and age are included. Authors: 1, Stanley and Fagerstrom 1974; 2, Frey *et al.* 1984; 3, Daley 1968; 4, Howard 1966; 5, Frey and Howard 1970; 6, Howard 1971; 7, Howard 1972; 8, Frey and Howard 1982; 9, Howard and Frey 1984; 10, Frey and Howard 1985a; 11, Frey and Howard 1985b; 12, Frey 1990; 13, Frey and Howard 1990; 14, Pemberton and Frey 1984; 15, Heinberg 1970; 16, Heinberg and Birkelund 1984; 17, Heinberg 1974; 18, Fürsich and Heinberg 1983; 19, Martino 1989; 20, Vialov 1962; 21, Haskell *et al.* 1965; 22, Webby 1968; 23, Gevers *et al.* 1971; 24, Bradshaw 1981.

- non 1990 *Ancorichnus capronus* Howard and Frey; Frey and Howard, p. 808, fig. 12 [copy of Frey 1990, fig. 7D], fig. 13.1 [= *Beaconites capronus*].
- non 1991 *Ancorichnus coronus* Frey *et al.*; Aceñolaza and Buatois, p. 96, pl. 2.1 [= *Taenidium barretti*], pl. 2.3 [indeterminate].
- non 1993 *Ancorichnus coronus* Frey *et al.*; Aceñolaza and Buatois, p. 188, fig. 4D [copy of Aceñolaza and Buatois 1991, pl. 2.1; = *Taenidium barretti*].
- non 1993 *Ancorichnus* aff. *coronus* Frey *et al.*; Mikuláš, p. 106, fig. 3d [= indeterminate].

*Diagnosis.* Cylindrical, weakly sinuous, sub- to horizontal burrow containing a central meniscate fill and a structured mantle (after Heinberg 1974).

*Type ichnospecies.* *Ancorichnus ancorichnus* Heinberg, 1974 (by monotypy)

*Remarks.* According to Heinberg and Birkelund (1984) *Muensteria* (*sensu lato*) includes the ichnogenus *Ancorichnus*. Whether they regarded *Ancorichnus* as an ichnosubgenus of *Muensteria*, or a synonym of *Muensteria*, is uncertain. However, *Muensteria* is now included within the unwalled ichnogenus *Taenidium* and, while both *Ancorichnus* and *Taenidium* are unwalled, the latter comprises a simple, one-stage backfill, whereas *Ancorichnus* has a two-stage fill comprising an inner meniscate fill and an outer mantle.

*Ancorichnus* is considered to be monospecific. *A. capronus* Howard and Frey, 1984, and *A. coronus* Frey *et al.* 1984, are now included within *Beaconites*.

*Ancorichnus ancorichnus* Heinberg, 1974

- 1970 Meniscus tunnel; Heinberg, p. 230, fig. 3e.
- \*1974 *Ancorichnus ancorichnus* Heinberg, p. 7, figs 1A, 2-4, 9A.



- 1983 *Ancorichnus ancorichnus* Heinberg; Fürsich and Heinberg, p. 94, fig. 7.II.  
 1984 *Muensteria* Sternberg; Heinberg and Birkelund, p. 365, fig. 10B.  
 ?1990 *Ancorichnus ancorichnus* Heinberg; Dam, p. 121, figs 4, 7A.  
 ?1990 *Ancorichnus ancorichnus* Heinberg; Dam, p. 221.  
 1990 *Ancorichnus ancorichnus* Heinberg; Bromley, p. 149, fig. 9.3.

*Diagnosis.* As for ichnogenus.

*Remarks.* The mantle in *Ancorichnus* is an integral part of the burrow fill, produced by the hydrostatic anchoring of the burrow producer. The mantle is not a wall structure. To avoid possible confusion with *Beaconites*, a structured mantle should be recognized or confidently inferred (*contra* the emendment by Frey *et al.* 1984).

*A. ancorichnus* has only been recorded from the Jurassic of Greenland (Text-fig. 4). This is probably because excellent preservation of the fabric in the mantle is required for it to be recognizable, and weathering of rock surfaces may be retarded in the high arctic. The mantle typically exhibits a structure formed by the preferred orientation of the sediment, and usually this is defined by oriented mica flakes (Heinberg 1974, fig. 4; Bromley 1990, fig. 9.1). Likewise, in Heinberg's (1974) specimens, the weakly arcuate menisci of the inner fill are defined by oriented mica flakes.

Determining whether a marginal structure is a mantle or a wall is difficult. However, the fabric in the mantle is oriented at an angle to the burrow boundary, as opposed to being normal to the direction of the burrow, which would be more characteristic of an applied wall lining. If internal structure in the mantle cannot be recognized, assignment to *Ancorichnus* is of course, problematic. Taphonomic variants (e.g. Dam 1990*a*, 1990*b*) may not contain a visibly structured mantle, but Dam's material was differentiated from *Beaconites* because the latter typically contains a lining (usually fine-grained) that differs in composition from the surrounding substrate. Dam (1990*a*, fig. 4) diagrammatically illustrated *A. ancorichnus* with *Janesonichnites heinbergi* Dam, 1990, as a compound specimen (*sensu* Pickerill 1994) and suggested that the two types of burrow represent different patterns of behaviour by the same organism.

#### Ichnogenus BEACONITES Vialov, 1962

- non* 1975 *Beaconites* Vialov; Häntzschel, p. W45, fig. 28.1 [copy of Gevers *et al.* 1971, fig. 2 = *Taenidium barretti*].  
 ?1976 *Beaconites* Vialov; Scott *et al.*, p. 4.  
*non* 1981 *Beaconites barretti* Bradshaw, p. 630, figs 17–18 [= *Taenidium barretti*].  
*non* 1984 *Beaconites* Vialov; Narbonne, p. 409, fig. 8G [= *Taenidium* cf. *serpentinum*].  
*non* 1985 *Beaconites barretti* Bradshaw; Bridge and Gordon, p. 173, fig. 8A–B [vertical burrow].  
*non* 1985 *Beaconites barretti* Bradshaw; Bridge and Droser, p. 154, fig. 8B [indeterminate vertical and horizontal structures].  
 ?1985 *Beaconites barretti* Bradshaw; Bridge and Nickelsen, p. 187.  
*non* 1987 *Beaconites barretti* Bradshaw; Brück, p. 259, figs 4–5 [= *Taenidium barretti*].  
 ?1988 *Beaconites* Vialov; Pollard, p. 339.  
*non* 1988 *Beaconites barretti* Bradshaw; Bradshaw and Webers, p. 787 [= *Taenidium barretti*].  
*non* 1990 *Beaconites* isp.; Dam and Andreasen, p. 208, fig. 11B [= *Taenidium barretti*].  
*non* 1990 *Beaconites barretti* Bradshaw; Woolfe, p. 302, fig. 3 [= *Taenidium barretti*].  
*non* 1992 *Beaconites barretti* Bradshaw; Tegan and Curran, p. A154 [= *Taenidium barretti*].  
*non* 1992 ?*Beaconites* Vialov; Pearson, p. 129, figs 3D–E [3D = *Taenidium barretti*, 3E indeterminate].

*Emended diagnosis.* Small, cylindrical, unbranched, walled, meniscate burrow. Straight or sinuous, horizontal or more rarely inclined or vertical. Weakly to strongly arcuate meniscate packets or segments enclosed by distinct, smooth and unornamented burrow linings.

*Type ichnospecies.* *Beaconites antarcticus* Vialov, 1962 (by monotypy).

*Remarks.* *Beaconites* has distinct but structureless walls and, to date, has not been recognized with a diameter exceeding 30 mm. Large, unlined, unlined meniscate trace fossils should not be included within this ichnogenus; *B. barretti*, is transferred to *Taenidium*. *A. coronns* and *A. capromis* have been transferred to *Beaconites* as distinctive ichnospecies, since the structure surrounding their central fill is a distinct wall or lining.

In addition to the records of *Beaconites* in the synonymy lists, other references to *Beaconites* have been included in tabulations by Pollard *et al.* (1982), Pollard (1988), and Maples and Archer (1989). Pollard *et al.* (1982) assigned the ichnofossils of Trewin (1976) and Berg (1977), amongst others, to *Beaconites*. Berg's (1977) specimens are indeterminate vertical burrows, whereas Trewin (1976) figured and described only *Scolicia* Quatrefages, 1849, and *Cruziana* Orbigny, 1842. Pollard (1988) reported the occurrence of *Beaconites* in mid-Jurassic cores from offshore Britain and also attributed trace fossils described by Stanistreet *et al.* (1980), to this ichnogenus. These latter traces, originally reported as *Rhizocorallium* Zenker, 1836, do not have marginal tubes, thereby excluding them from a rhizocoralliid designation. Assignment to *Beaconites* is also doubtful following the comment of Stanistreet *et al.* (1980) that although the burrows are more than 200 mm wide, they are only 10–20 mm in depth, suggesting that these traces are surficial trails, not cylindrical backfilled structures. Maples and Archer (1989) included reference to Gevers and Twomey (1982)—a report that mentioned structures of Haskell *et al.* (1965)—and reference to an abstract by Plume (1983), that does not name any ichnofossils.

O'Sullivan *et al.* (1986) noted 'Beaconites-like' burrows (that they distinguished from the ichnogenus by a passive burrow fill) and Bamford *et al.* (1986) noted 'Beaconites-type' burrows that in fact contained distinct walls and lacked internal menisci. Allen and Williams (1981a) also reinterpreted 'mechanical structures' of Dixon (1921), Allen (1961, 1963), Dineley (1966) and Horne and Gardiner (1973), as large burrows attributable to *Beaconites*. Horne and Gardiner (1973), however, correctly considered their specimens to be most similar to *Kulindrichnus* Hallam, 1960, a trace fossil subsequently placed in synonymy with *Berganeria langi* (Hallam, 1960) by Pemberton *et al.* (1988). The examples of the other authors are of uncertain meniscate backfill. Finally, other authors have included reference to *Beaconites* when commenting upon possible synonymies for meniscate trace fossils. Frey *et al.* (1984) and Squires and Advocate (1984) considered including it within other unlined meniscate burrows, and D'Alessandro and Bromley (1987) within an ichnotaxon comprising weakly walled or unlined meniscate burrows.

#### *Beaconites antarcticus* Vialov, 1962

- \*1962 *Beaconites antarcticus* Vialov, p. 726, figs 9–10.
- 1965 *Beaconites antarcticus* Vialov; Haskell *et al.*, p. 243.
- 1968 *Beaconites antarcticus* Vialov; Webby, p. 1004, fig. 7.
- 1971 *Beaconites antarcticus* Vialov; Gevers *et al.*, p. 81, pl. 18, fig. 3.
- non 1971 *Beaconites antarcticus* Vialov; Gevers *et al.*, p. 81, pl. 18, figs 1–2, 4 [= *Taenidium barretti*].
- ?1975 Meniscate burrow; Edwards, p. 7, fig. 1.
- non 1976 *Beaconites* cf. *antarcticus* Vialov; Pollard, p. 105 [= *Taenidium barretti*].
- ?1977 *Beaconites antarcticus* Vialov; McKelvey *et al.*, p. 829.
- ?1977 *Beaconites antarcticus* Vialov; Forsyth and Chisholm, p. 19.
- ?1978 *Beaconites antarcticus* Vialov; Allen, p. 88.
- ?1978 *Beaconites antarcticus* Vialov; Williams, p. 96.
- ?1978 *Beaconites antarcticus* Vialov; Allen and Williams, p. 121.
- ?1979 *Beaconites antarcticus* Vialov; Allen, p. 70.
- non 1980 *Beaconites antarcticus* Vialov; Bridge *et al.*, p. 154, pl. 2D–E [2D = *Bergaueria*; 2E is indeterminate].
- non 1981 *Beaconites antarcticus* Vialov; Allen and Williams, p. 23, fig. 6A [indeterminate vertical burrow].
- non 1981 *Beaconites antarcticus* Vialov; Allen and Williams, p. 255, figs 2, 4–11 [2, 4–5 are vertical burrows; 6–11 = *Taenidium barretti*].
- 1981 *Beaconites antarcticus* Vialov; Bradshaw, p. 630, fig. 15 [? fig. 16].

- non 1982 *Beaconites antarcticus* Vialov; Graham and Pollard, p. 259, figs 3A–B, 4A–C, 5A–B. [= *Taenidium barretti*].
- ?1985 *Beaconites antarcticus* Vialov; Bridge and Gordon, p. 170, fig. 8c.
- ?1985 *Beaconites antarcticus* Vialov; Bridge and Nickelsen, p. 187.
- non 1985 cf. *Beaconites antarcticus* Vialov; Eagar *et al.*, p. 134, pl. 14A [= *Taenidium barretti*].
- non 1985 *Beaconites antarcticus* Vialov; Brück *et al.*, p. 87, figs 4A–B, 5A–B [vertical burrows].
- non 1988 *Beaconites antarcticus* Vialov; Gordon, p. 143, figs 4A–B [= *Taenidium isp.*].
- ?1990 *Beaconites antarcticus* Vialov; Woolfe, p. 302, figs 3–4.
- ?1993 *Beaconites antarcticus* Vialov; Ékes, p. 469.

*Emended diagnosis.* Small, cylindrical, unbranched, lined burrows, straight to slightly sinuous. Burrow infill meniscate, typically heterogeneous packets of unequal thickness. Larger packets slightly thicker to slightly thinner than overall burrow width, meniscate interfaces weakly to moderately arcuate. Burrow lining is uniform, smooth and unornamented, commonly thick and very distinct.

*Remarks.* As noted by D'Alessandro and Bromley (1987), *B. antarcticus* has sediment packets of unequal length. Commonly, specimens are encountered where thicker packets have been preferentially weathered out, preserving only thin compartments, or 'septa' (e.g. Vialov 1962; Gevers *et al.* 1971). The burrows of McKelvey *et al.* (1977), Forsyth and Chisholm (1977), Allen (1978, 1979), Williams (1978), Allen and Williams (1978) and Ékes (1993) were not illustrated nor adequately described and possibly correspond to additional examples of *T. barretti*. The burrow of Edwards (1975) is insufficiently illustrated to determine confidently whether the specimen is walled or unwalled.

*Beaconites capronus* (Howard and Frey, 1984) comb. nov.

- 1966 Chevron trail; Howard, p. 40, fig. 4.
- 1970 Chevron burrow; Frey and Howard, p. 183, fig. 8A [copy of Howard 1966, fig. 4].
- 1971 Chevron trail; Howard, p. 180, fig. 11 [*partim*; copy of Howard 1966, fig. 4].
- 1972 Chevron trail; Howard, p. 217, fig. 1 [copy of Howard 1966, fig. 4].
- 1982 Chevron burrow; Frey and Howard, p. 3, fig. 2c [copy of Howard 1966, fig. 4].
- \*1984 *Ancorichnus capronus* Howard and Frey, p. 201, figs 2–3.
- 1984 *Ancorichnus capronus* Howard and Frey; Frey *et al.*, p. 514.
- 1985 *Ancorichnus capronus* Howard and Frey; Frey and Howard, p. 373, figs 5.6, 5.8, 16.3D.
- 1985 *Ancorichnus capronus* Howard and Frey; Frey and Howard, p. 122, fig. 2 [copy of Howard and Frey 1984, fig. 2].
- 1985 *Ancorichnus capronus* Howard and Frey; Frey and Pemberton, p. 90, fig. 26 [copy of Howard and Frey 1984, fig. 2].
- 1989 *Ancorichnus capronus* Howard and Frey; Martino, p. 393, fig. 5.5.
- 1990 *Ancorichnus capronus* Howard and Frey; Frey, p. 204, fig. 7D.
- 1990 *Ancorichnus capronus* Howard and Frey; Frey and Howard, p. 808, fig. 12 [copy of Frey 1990, fig. 7D], fig. 13.1.

*Diagnosis.* Thinly lined, smooth walled, predominantly horizontal cylindrical burrow with distinct chevron-laminated fill (after Howard and Frey 1984).

*Remarks.* This ichnospecies is readily distinguishable by the chevron pattern of the meniscate fill. This fill has frequently been described as comprising alternating coarse and fine chevron-shaped packets of sediment (Howard and Frey 1984; Frey and Howard 1985a, 1985b, 1990), although alternating grain size is not necessarily ubiquitously present (e.g. Martino 1989). Howard (1966) described a chevron trail preserved in convex epirelief that he interpreted as having been formed at the sediment–water interface, probably by a gastropod. Subsequently the trace was considered to be a burrowed structure (Frey and Howard 1970, 1982) and included within *A. capronus* by Howard and Frey (1984). *B. capronus* has, to date, only been recognized in marine strata (Text-fig. 4).

*Beaconites coronus* (Frey *et al.*, 1984) comb. nov.

- 1968 *Meniscus* burrow; Daley, p. 124, fig. 12A [*partim*].  
 1974 Horizontal burrows; Stanley and Fagerstrom, p. 70, figs 6, 7A-B.  
 1984 *Muensteria* Sternberg; Pemberton and Frey, p. 291, figs 4.6, 5B.  
 \*1984 *Ancorichnus coronus* Frey *et al.*, p. 511, figs 1D [copy of Stanley and Fagerstrom 1974, fig. 6], 1E, 3A-C.

*Emended diagnosis.* Predominantly horizontal, more rarely inclined to vertical, distinctly lined, gently winding, small meniscate burrow. Relatively short (with respect to burrow width) meniscate packets, or segments, of alternating sediment type. Menisci gently to moderately arcuate.

*Remarks.* This ichnospecies is distinguished from *B. antarcticus* by its more uniformly sized and thin individual meniscate segments, and from *B. capromus* by the presence of gently to moderately arcuate menisci. Typically, several segments occupy a length of the burrow equivalent to its overall width. Only one of Daley's (1968) meniscate trace fossils appears to retain evidence of a wall structure. This structure, like the *Taenidium* of Toots (1967), may be due to preferential cementation of the sediment adjacent to the trace-fossil boundary and not be a wall structure or part of the trace fossil at all.

## Ichnogenus TAENIDIUM Heer, 1887

- ?1833 *Muensteria hoessii* Sternberg, p. 33, pls 6.4, 7.3 [*partim*] [= *Taenidium* isp., non *Chondrites*].  
 ?1833 *Muensteria flagellaris* Sternberg, p. 33, pl. 8.3 [indeterminate].  
 non 1833 *Muensteria geniculata* Sternberg, p. 33, pl. 6.3 [= *Hydrancylus* isp. by Nathorst 1880; ? = *Zoophycos* isp.].  
 1841 *Muensteria schneideriana* Göppert, p. 115, pl. 57.3 [= *Taenidium* isp.].  
 non 1851 *Muensteria annulata* Schafhäütl, pp. 22, 140, pl. 8.9 [= *T. fischeri* according to Heer 1877; ? = *Cladichnus* isp.].  
 1858 *Muensteria (Eumuensteria) flagellaris* Sternberg; Fischer-Ooster, p. 36.  
 1858 *Muensteria (Keckia) hoessii* Sternberg; Fischer-Ooster, p. 38, pls 7.3, 16.4 [= *Taenidium* isp.], 16.5 [= *Taenidium* isp. *partim*].  
 non 1858 *Muensteria (Keckia) dilatata* Fischer-Ooster, p. 39, pl. 2 [? = *Zoophycos* isp.].  
 1861 *Muensteria cretacea* Ooster, p. 69, pl. 11.24 [reported in Heer 1877].  
 non 1865 *Muensteria annulata* Schafhäütl; Heer, p. 244, pl. 10.8 [= *T. fischeri* according to Heer 1877; = *Cladichnus* isp.].  
 non 1869 *Muensteria* Sternberg; Ooster, p. 29, pls 8.2-8.4 [8.2 = *Spirophycus*; 8.3 ? = *Cladichnus fischeri*; 8.4 ? = *Ophiomorpha*].  
 1869 *Muensteria* Sternberg; Schimper, p. 194.  
 ?1877 *Muensteria (Keckia) antiqua* Sternberg; Heer, p. 116, pl. 43.22.  
 ?1877 *Muensteria (Eumuensteria) flagellaris* Sternberg; Heer, p. 116, pls 66.4-66.5.  
 1877 *Muensteria cretacea* Ooster; Heer, p. 144, pl. 57.6 [= *Taenidium* isp.].  
 ?1877 *Muensteria (Keckia) nummulitica* Heer, p. 163, pl. 69.4.  
 1877 *Muensteria (Keckia) hoessii* Sternberg; Heer, p. 164, pls 66.6, 69.3 [= *Taenidium* isp.].  
 ?1877 *Muensteria (Keckia) dilatata* Fischer-Ooster; Heer, p. 164.  
 non 1880 *Taenidium alysiodes* Hosius and von der Marck, p. 131, pl. 24.5 [? = alga].  
 non 1887 *Muensteria annulata* Schafhäütl; Squinabol, p. 554, pl. 17.3 [and synonymies therein; = *T. fischeri* according to Squinabol 1891; ? = *Cladichnus fischeri*].  
 non 1887 *Muensteria isseli* Squinabol, p. 555, pl. 17.4-17.5 [= *T. fischeri* according to Squinabol 1891; ? = *Cladichnus fischeri*].  
 1887 *Muensteria minima* Squinabol, p. 555, pl. 16.5 [? = *Cladichnus* isp.].  
 ?1888 *Taenidium carboniferum* Sacco, p. 162, pl. 2.1.  
 ?1888 *Muensteria flagellaris* Sternberg; Sacco, p. 169.  
 non 1888 *Muensteria annulata* Schafhäütl; Sacco, p. 170 [= *T. fischeri* according to Squinabol 1891; = *Cladichnus* isp.].



- 1888 *Muensteria minima* Squinabol; Sacco, p. 170.  
 non 1888 *Muensteria isseli* Squinabol; Sacco, p. 170 [= *T. fischeri* fide Squinabol 1891; = *Cladichnus fischeri*].
- ?1890 *Taenidium helveticum* Schimper and Schenk, p. 54, fig. 42.2.  
 non 1894 *Taenidium radiatum* Schröter, p. 80, figs 1–2 [= *Cladichnus fischeri*].  
 non 1941 *Taenidium isseli* Squinabol; Papp, p. 315, figs 1–2 [= *Cladichnus fischeri*].  
 1955 *Muensteria* Sternberg; Seilacher, fig. 5.43.  
 1958 *Muensteria* Sternberg; Seilacher, p. 1070, table 2.28.  
 1958 *Muensteria hoessii* Sternberg; Seilacher, p. 1070, table 2.40 [= *Taenidium* isp.].  
 non 1962 *Taenidium* Heer [*partim*]; Häntzschel, p. W218 [non figs 136.2a–136.2b (copies of Papp, 1941, fig. 1) = *Cladichnus fischeri*].  
 1962 *Muensteria hoessii* Sternberg; Seilacher, p. 229, pl. 2.6 [= *Taenidium* isp.].  
 1964 *Muensteria* Sternberg; Seilacher, p. 309, fig. 7.27.  
 ?1967 *Taenidium* Heer; Toots, p. 93, fig. 1.  
 1971 *Taenidium* Heer; Perkins and Stewart, p. 77, fig. 57d.  
 ?1971 *Taenidium* Heer; Chamberlain, p. 42, fig. 6.32 [? = *Cladichnus* isp., *partim*, ? = *Rhabdoglyphus* isp., *partim*].
- non 1971 *Taenidium annulata* (Schafhäutl); Chamberlain, p. 241, figs 81–L, [? = *Cladichnus*] pl. 32.12 [? = *Rhabdoglyphus*].  
 1972 *Taenidium* Heer; Germs, p. 866, pls 2.2–2.3.  
 1974 *Muensteria* Sternberg; Heinberg, p. 17, fig. 1.  
 non 1975 *Munsteria* [= *lapsus calami*]; Chamberlain, p. 1076, fig. 2F'.  
 1975 *Taenidium* Heer; Chamberlain, p. 1076, fig. 2G'.  
 1975 *Keckia* Glocker; Häntzschel [*partim*], p. W75 [non fig. 47.2, copy of Glocker 1841, pl. 4].  
 1975 *Muensteria* Sternberg; Häntzschel [*partim*], p. W84.  
 1975 *Taenidium* Heer; Häntzschel, [*partim*], p. W112 [non fig. 70.1 = *Cladichnus fischeri*].  
 ?1976 ?*Taenidium* Heer; Hakes, p. 38, pl. 11.6 [also tabulated in Hakes 1985].  
 1977 *Muensteria* cf. *M. hoessii* Sternberg; Chamberlain, p. 14, figs 2L, 5E [? = *Taenidium barretti*].  
 1977 *Taenidium serpentium* [*lapsus calami*]; Chamberlain, p. 18, fig. 3F [= *Taenidium* isp.].  
 1977 *Keckia annulata* Glocker; Książkiewicz, p. 63, pl. 3.14 [= *Taenidium* isp.].  
 1977 *Keckia hoessii* (Sternberg); Książkiewicz, p. 64, pls 3.15–3.16 [= *Taenidium* isps.].  
 1977 *Taenidium annulatum* (Schafhäutl); Książkiewicz, p. 85, pl. 5.4 [= *Taenidium* isp.].  
 non 1977 *Taenidium isseli* (Squinabol); Książkiewicz, p. 85, pls 5.1–5.2 [= *Cladichnus* isp.].  
 1977 *Muensteria geniculata* Sternberg; Książkiewicz, p. 122, pl. 13.2 [? = *Taenidium barretti*].  
 non 1977 *Muensteria hamata* Fischer-Ooster; Książkiewicz, p. 122, pl. 13.3 [indeterminate branching meniscate structure].
- ?1977 *Muensteria planicostata* Książkiewicz, p. 122, pl. 13.1 [? surface trail].  
 1977 *Taenidium* Heer; Stanley *et al.* p. 267, fig. 18 [*partim*], fig. 19c.
- non 1978 *Taenidium annulatum* (Schafhäutl); Alexandrescu and Brustur, p. 21, pl. 2.5 [= *Cladichnus fischeri*].
- non 1978 *Taenidium* isp.; Alexandrescu and Brustur, p. 21, pl. 3.1 [= *Cladichnus fischeri*].  
 1978 *Muensteria* Sternberg; Chamberlain, p. 144, fig. 3B.  
 1978 *Taenidium* Heer; Chamberlain, p. 52, figs 4.23 [non 4.24 = *Cladichnus*], 10 [*partim*], 11 [*partim*, copy of Chamberlain 1971, fig. 6].  
 1978 *Taenidium* Heer; Seilacher, p. 195, fig. 6.30.  
 ?1978 *Taenidium* Heer; Carey, p. 438, fig. 6.  
 1979 *Muensteria* Sternberg; Chamberlain p. 12, fig. 3 [copy of Chamberlain 1977, fig. 2].  
 1979 *Keckia* isp.; McCarthy, p. 363, figs 3A, 3C–E.  
 1980 *Taenidium* Heer; Pickerill, p. 1270, fig. 4f.  
 ?1982 *Taenidium* Heer; MacDonald, p. 9, figs 6A–B.  
 ?1982 *Taenidium* Heer; Tevesz and McCall, p. 270, fig. 5 [copy of Toots 1967, fig. 1].  
 1983 *Muensteria* Sternberg; Wetzel, p. 290, fig. 2 [*partim*], fig. 6.4.  
 1984 *Muensteria* Sternberg; Howard and Frey, p. 201, fig. 1.
- non 1984 *Muensteria* Sternberg; Pemberton and Frey, p. 291, figs 4.6, 5B [= *Beaconites coronis*].  
 1984 *Muensteria* Sternberg; Pickerill *et al.*, p. 265, fig. 6A.  
 non 1984 *Muensteria* Sternberg; Heinberg and Birkelund, p. 365, fig. 10B [= *Ancorichnus ancorichnus*].  
 ?1984 Backfilled burrows; Archer, p. 286, fig. 3C.

- 1985 *Entradichnus meniscus* Ekdale and Picard, p. 8, pl. 2A–B.  
 1985 *Muensteria* Sternberg; Eagar *et al.*, p. 140, pls 1B [partim], 6C.  
 1985 *Muensteria* Sternberg; Frey and Pemberton, p. 76, fig. 2 [copy of Howard and Frey 1984, fig. 1].  
 1985 *Muensteria* Sternberg; Frey and Howard, p. 130, fig. 9 [copy of Howard and Frey 1984, fig. 1].  
 1985 *Muensteria* isp.; Frey and Howard, p. 378, figs 10.12, 16.3b, 19.6.  
 ?1986 *Taenidium* Heer; Miller, p. 343, fig. 3b.  
 1986 *Muensteria* isp.; Valenzuela *et al.*, p. 129.  
 1986 *Muensteria* Sternberg; Wheatcroft, p. 61, pl. 6.1c.  
 1986 *Keckia* isp.; Wheatcroft, p. 61, pl. 6.1b.  
 1986 *Muensteria* Sternberg; Brenchley *et al.*, p. 246.  
 1987 *Muensteria* isp.; Narbonne *et al.*, p. 1284.  
 non 1987 *Muensteria* isp.; Pickerill *et al.*, p. 83, fig. 4D [indeterminate].  
 1987 '*Muensteria*'; D'Alessandro *et al.*, p. 287, fig. 3.  
 1987 *Muensteria* isp.; Lockley *et al.*, p. 259, figs 1, 2b.  
 ?1987 ?*Margaritichnus* isp.; Lockley *et al.*, p. 258, fig. 3.  
 1987 Backfilled burrow; Narbonne and Hofmann, p. 671, fig. 10e.  
 1988 *Taenidium* Heer; Bjerstedt, p. 55, fig. 5f.  
 1988 *Muensteria* isp.; Pickerill and Harland, p. 125, fig. 4d.  
 1988 *Muensteria geniculata* Sternberg; McCann and Pickerill, p. 337, fig. 4.4 [= *Taenidium* isp.].  
 1988 *Muensteria* isp.; McCann and Pickerill, p. 337, fig. 4.5.  
 non 1988 *Taenidium isselei* Squinabol; McCann and Pickerill, p. 342, fig. 5.8 [= *Cladichnus* isp.].  
 1988 *Muensteria* Sternberg; Widman and Feldmann, p. 535, fig. 2.4.  
 1988 *Beaconites antarcticus* Vialov; Gordon, p. 144, figs 4A–B.  
 non 1989 *Taenidium* Heer; Powichrowski, p. 392, fig. 12 [= *Cladichnus* isp.].  
 1989 *Muensteria* isp.; Walter *et al.*, p. 232, fig. 9A.  
 1990 *Muensteria* Sternberg; Dam and Andreassen, p. 215, fig. 11c.  
 1990 *Muensteria* cf. *geniculata* Sternberg; Mikuláš, p. 314, fig. 1a, pl. 2.4.  
 1991 *Taenidium* Heer; Burton and Link, p. 295, figs 7A, 7G.  
 1991 *Taenidium* Heer; Ekdale and Bromley, p. 232, figs 1, 3, 4A, 5, 7, 12.  
 ?1991 *Taenidium* Heer; Miller, p. 167, fig. 4H [copy of Miller 1986m, fig. 3B].  
 ?1991 *Taenidium* Heer; Miller, p. 76, fig. 4.  
 ?1991 *Taenidium* Heer; Romano, p. 197.  
 ?1991 *Taenidium* Heer; Scasso *et al.*, p. 251.  
 1991 *Muensteria* Sternberg; Leszczyński, p. 171, figs 4, 6 [partim].  
 1992 *Taenidium* isp.; Crimes *et al.*, p. 68, figs 4D, 5C.  
 ?1992 ?*Taenidium* Heer; Mikuláš, p. 225, pl. 2.3.  
 ?1993 *Taenidium* Heer; Smith *et al.*, p. 590, fig. 13.

*Etended diagnosis.* Variably oriented, unwalled, straight, winding, curved, or sinuous, essentially cylindrical, meniscate backfilled trace fossils. Secondary successive branching may occur, but true branching is absent.

*Type ichnospecies.* *T. serpentinum* Heer, 1877.

*Remarks.* Wall linings are not present in *Taenidium*, distinguishing it as an unwalled ichnotaxon (see previous discussion). The trace fossil may typically appear slightly annulate when thick meniscate packets are present; otherwise, the boundary is usually slightly irregular. Fill is variable, of homogeneous or heterogeneous, faecal and non-faecal content. Ichnospecies are defined by such variations in the style of meniscate fill.

Only three valid ichnospecies of *Taenidium* were described by D'Alessandro and Bromley (1987), *T. serpentinum*, *T. satanassi* and *T. cameronensis*. *T. gillieroui* Heer, 1877, and *T. convolutum* Heer, 1877 were considered synonymous with the type. In this contribution we designate a fourth ichnospecies, *T. barretti*.

D'Alessandro and Bromley (1987) also noted that *M. clavata* Sternberg, 1833, *M. vermicularis* Sternberg, 1833 and *M. lacunosa* Sternberg, 1833 are not trace fossils. They also made *T. fischeri* the type of a new ichnogenus, *Cladichnus*, included within which were specimens of *T. lusitanicum* Heer,

1881 by Heer (1881) and Wilkens (1947); *M. (K.) annulata* by Fischer-Ooster (1858 *partim*); *T. annulata* by D'Alessandro *et al.* (1986) and 'Taenidium' by Kern (1978) and Pedersen and Surlyk (1983). Also included should be references of *T. fischeri* by Sacco (1888), Schimper and Schenk (1890), Squinabol (1891), Schröter (1894) and Liburnau (1900). Together with *M. bicornis* Heer, 1877, *M. caprina* Heer, 1877 and *M. involutissima* Sacco, 1888 that were placed within *Spriophycus* Häntzschel, 1962 by Häntzschel (1962), *M. clavata*, *M. verrucularis*, *M. lacunosa* and *T. fischeri* are not included in the above synonymy list.

A plethora of other potential synonyms also exist between the various ichnospecies of *Taenidium* and *Muensteria*, and with other ichnogenera. Briefly, Fischer-Ooster (1858) included *Keckia annulata* Glocker, 1841, within one of his 'subgenera' of *Muensteria*, namely *M. (Keckia) annulata* Schafhäütl, 1851. *M. annulata* and *M. isseli* Squinabol, 1887 were considered similar to *T. fischeri*, by Heer (1877) and Squinabol (1891) respectively. *Keckia* and *Saportia* Squinabol, 1891, were included within Wilken's (1947) discussion of *Taenidium*. Subsequently, D'Alessandro and Bromley (1987) considered *Keckia* as a dubious ichnotaxon, and included *Saportia* within *Cladichmus*. Most specimens of *Keckia* can therefore be accommodated within *Cladichmus*.

Another of Fischer-Ooster's (1858) 'subgenera', containing mainly spreiten-like structures, was *Muensteria (Hydrancyllus)*. The subgenus included *M. (H.) geniculata* Sternberg, 1833. *Hydrancyllus* was later (Nathorst 1880) considered to be a distinct ichnogenus but can most probably be considered a junior synonym of *Zoophycos* Massalongo, 1855. Książkiewicz's (1977) interpretation of *Muensteria* was generally analogous to Fischer-Ooster's (1858) *Hydrancyllus* subgenus. However, Książkiewicz's (1977) specimen of *M. geniculata*, as well as *M. geniculata* of McCann and Pickerill (1888) and Mikuláš (1990), contained almost semi-circular menisci as opposed to a spreite, and must be reassigned within *Taenidium*.

D'Alessandro and Bromley (1987) also considered *M. cretacea* Ooster, 1861, *M. hoessii* Heer, 1877, *M. planicostata* Książkiewicz, 1977, *T. carboniferum* Sacco, 1888, and *T. meandriiformis* Müller, 1966 to be dubious ichnospecies. Of these, *M. planicostata*, in its original diagnosis, was stated as hypichnial and described as 'crescent grooves produced by contraction of (a gastropod) foot, later cast in sand' (Książkiewicz 1977, p. 122). Being in all likelihood a surface trail, it should not be included within *Taenidium*. *T. meandriiformis*, like *T. praecarbonicum* Gumbel, 1879 into which the former was placed as a junior synonym by Pfeiffer (1966), is herein considered synonymous with *T. serpentinum*. Sacco's (1888) *T. carboniferum* is similar to the structures of Lockley *et al.* (1987) that they erroneously termed ?*Margaritichmus* Bandel, 1973; they should not be included under *Eione* as suggested by Maples and Suttner (1990), *Eione* being invalid as an ichnotaxon (Rindsberg 1990). In subdued convex epirelief or concave hyporelief, these trace fossils resemble *T. serpentinum*, but although their structure is distinctly annulate, packets are occasionally elliptical as opposed to bullet-shaped in form, and in longitudinal cross-section the upper parts of the backfilling packets are imbricated. Imbrication and the occasional elliptical packeting (i.e. where no menisci are really observed) may ultimately preclude inclusion of this form within *Taenidium*, and the ichnospecies is considered dubious. *M. cretacea* has characteristics similar to some specimens of *M. hoessii*, and is similarly still considered a dubious ichnospecies. The original *M. hoessii* and *M. flagellaris* Sternberg, 1833 were considered to resemble *Chondrites* by D'Alessandro and Bromley (1987) because they were diagnosed as dichotomous. From Sternberg (1833, pls 6.4, 8.3), however, it is uncertain whether his specimens exhibited false or secondary successive branching, and his other illustration of *M. hoessii* (pl. 7.3) is of an unbranched specimen. The original diagnosis and illustrations of *M. hoessii* additionally mentioned the presence of 'lineis transversis' and exhibit a distinct meniscate structure, unlike *Chondrites*.

*M. hoessii* is, however, a name that has been used for several different types of burrow and some specimens may ultimately represent distinct ichnospecies (D'Alessandro and Bromley 1987). Informally, it appears that the burrows *M. cf. hoessii* of Chamberlain (1977), (?)*Taenidium* of Carey (1978) and *Muensteria* of Wiedman and Feldmann (1988) contain a highly distinct, heterogeneous backfill in which regularly spaced segments form striking crescentic compartments between infill that is indistinguishable from the enclosing strata. *K. annulata* and *K. hoessii* of Książkiewicz (1977,



pls 3.14, 3.16) and *Keckia* isp. of McCarthy (1979, fig. 3c) are similar to *B. capronus* apart from lacking a wall. Longitudinally thin, equally spaced, deeply concave, densely stacked but very distinct heterogeneous meniscate segments would seem to distinguish *M. (K.) hoessii* of Fischer-Ooster (1858, pl. 16.4), *M. cretacea* of Heer (1877), *M. hoessii (partim)* of Heer (1877), and *M. hoessii* of Seilacher (1958, 1962). We therefore concur with D'Alessandro and Bromley (1987) that additional ichnospecies of *Taenidium* can probably be distinguished. Apart from *T. barretti* introduced herein, however, we have not attempted to investigate thoroughly other potential ichnospecies of *Taenidium*, as this is beyond the scope of this contribution. Such material has been retained in the ichnogenetic synonymy only.

Ekdale and Bromley (1991) also illustrated both the densely meniscate and strikingly segmented forms of *Taenidium* occurring in association with *Zoophycos*. Their photographs additionally illustrate the problems that can arise between these two ichnotaxa when seen in section, because both may appear as unwalled, meniscate (or spreiten) structures. Slabbing of samples may be necessary to distinguish the two (Chamberlain 1978a). The ichnogenus *Compaginaticmus* Pickerill, 1989, was erected for burrows that contain similar arcuate meniscate infill to *Taenidium*. However, at the base of this burrow, underlying the meniscate infill, is a distinct coprolitic, pelletal layer. The burrow therefore contains a compound fill of upper meniscate segments and lower pelletal layer. Recognition of both types of fill is necessary for the correct identification of this ichnotaxon; otherwise, if the burrow was entirely meniscate, it would be included within *Taenidium* (Pickerill 1989). Full relief views *Arthropycus* Hall, 1852, and *Planolites annularius* Walcott, 1980, may also give the impression of being meniscate and could be confused with *Taenidium*, as could *Nereites* MacLeay, 1839, where the disturbance zone in the latter is not preserved (D'Alessandro and Bromley 1987). Again, slabbing of samples is essential to confirm that the trace fossil being identified is a burrow and not a trail, and that the infill is entirely meniscate, and not partly pelletal, internally structureless or imbricate, nor externally disturbing the surrounding sediment. *Imponoglyphus* Vialov, 1971, contains truncated cones invaginated into one another. Poorly preserved or weathered material may potentially appear as simple, articulated meniscate segments assignable to *Taenidium*. Another invaginate trace fossil, *Rhabdoglyphus* Vassoievich, 1951, resembles material figured by Chamberlain (1971a, pl. 32.12) as unbranched *T. annulata* (see Stanley and Pickerill 1993 for discussion).

#### *Taenidium serpentinum* Heer, 1877

- 1858 *Muensteria (Keckia) schneideriana* Göppert; Fischer-Ooster, p. 39, pl. 15.3.
- \*1877 *Taenidium serpentinum* Heer, p. 116, pls 46.3–46.4.
- 1877 *Taenidium gillieronii* Heer, p. 117, pl. 50.1 [partim].
- 1877 *Taenidium convolutum* Heer, p. 117, pl. 50.2 [partim].
- 1887 *Muensteria serpentina* [= *lapsus calami*]; Maillard, p. 37, pl. 1.4.
- 1890 *Taenidium serpentinum* Heer; Schimper and Schenk, p. 54, fig. 42.1.
- ?1966 *Taenidium maeandriiformis* Müller, p. 712, figs 1–2, pl. 1.
- ?1966 *Taenidium praecarbonicum* Gümbel; Pfeiffer, p. 688, fig. 3.21.
- ?1971 *Taenidium serpentinum* [= *lapsus calami*]; Chamberlain, p. 42, fig. 6.32 [partim].
- 1971 *Taenidium serpentinum* [= *lapsus calami*]; Chamberlain, p. 241, pl. 32.10.
- ?1972 *Taenidium carbonicum* [= *lapsus calami*]; Häntzschel, p. 115, fig. 3.
- 1974 *Muensteria* Sternberg; Fürsich, p. 34, figs 28, 29a.
- ?1977 *Taenidium serpentinum* [= *lapsus calami*]; Chamberlain, p. 18, figs 2a, 2h, 3F 7A [non 3i = *Taenidium* isp.].
- ?1982 *Taenidium praecarbonicum* Gümbel; Benton, p. 122, fig. 6v.
- 1987 *Taenidium serpentinum* Heer; D'Alessandro and Bromley, p. 743, figs 5–7.
- ?1989 *Taenidium serpentinum* Heer; Miller, p. 48, fig. 2b.
- 1990 *Taenidium serpentinum* Heer; Dam, p. 142, fig. 11a [partim].
- ?1990 *Taenidium serpentinum* Heer; Maples and Suttner, p. 874, fig. 14.1.
- 1990 *Taenidium serpentinum* Heer; Dam, p. 226, fig. 6 [partim copy of Dam, 1990, fig. 11a], figs 15, 19, 23.



*Diagnosis.* Serpentine *Taenidium* having well-spaced, arcuate menisci; distance between menisci about equal to or a little less than burrow width. External moulds may show slight annulation corresponding to menisci, or fine transverse wrinkling. Secondary subsequent branching and intersections occur. Boundary sharp and lacks lining (after D'Alessandro and Bromley 1987).

*Remarks.* As with *T. satanassi*, this ichnospecies has meniscate packets typically of slightly less length than width. Unlike *T. satanassi*, however, the fill is homogeneous and of the same composition as the enclosing strata. The possibility of a thin, incomplete, and generally 'insignificant' lining occurring locally was indicated by D'Alessandro and Bromley (1987). This should not affect the naming of the structure, since trace fossils are named after their predominant features (Pickerill 1994), in this case the lack of a wall structure. *T. praecarbonicum* is provisionally included within *T. serpentinum* (along with specimens of *T. gilleroni*, and *T. convolutum*), although sketches of the former (Heer 1877; Pfeiffer 1966; Benton 1982) would indicate that assignment is dubious, since the individual sediment packets are ellipsoidal in shape and nowhere have concave meniscate interfaces. To date, the ichnospecies has only been confirmed in marine sediments (Text-fig. 5).

*Taenidium satanassi* D'Alessandro and Bromley, 1987

- 1986 *Muensteria* isp. Sternberg; D'Alessandro *et al.*, p. 299, fig. 5b.
- \*1987 *Taenidium satanassi* D'Alessandro and Bromley, p. 743, figs 6, 8–9.
- 1990 *Taenidium satanassi* D'Alessandro and Bromley; Bromley, p. 178, fig. 10.9 [copy of D'Alessandro and Bromley 1987, fig. 8].
- 1990 *Taenidium satanassi* D'Alessandro and Bromley; Frey and Howard, p. 15, fig. 16.13, fig. 25 [copy of Howard and Frey 1984, fig. 1].

*Diagnosis.* Sinuous to nearly straight backfilled burrows, the fill consisting of meniscate packets, each packet containing two types of sediment of more or less equal thickness; sediment packets considerably shorter than wide. Menisci weakly arcuate (after D'Alessandro and Bromley 1987).

*Remarks.* Typically a slight constricting annulation in the outer boundary of the burrow corresponds to the contact between the packets. *T. barretti*, although similarly containing a heterogeneous fill, does not have distinct packeting but only short, more arcuate crescents or non-compartmentalized meniscate fill. Frey and Howard's (1990) specimens do not incorporate alternating meniscate fill, although individual packets are considerably shorter than wide. The few specimens so far encountered of this ichnospecies are from a marine setting (Text-fig. 5).

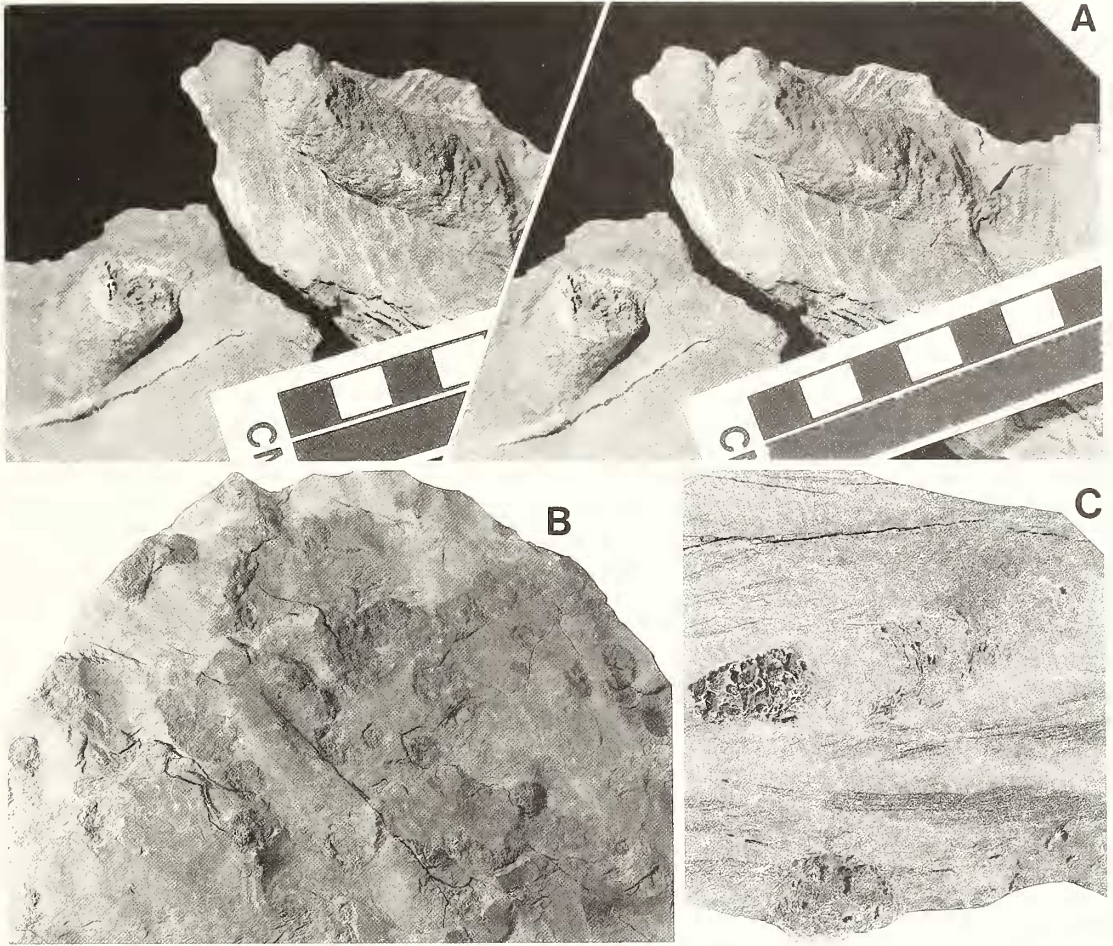
*Taenidium cameronensis* (Brady, 1947)

- \*1947 *Scolecocoprns cameronensis* Brady, p. 471, pl. 69, fig. 1.
- 1955 *Scolecocoprns cameronensis* Brady; Lessertisseur, p. 58, fig. 33c [copy of Brady, pl. 69].
- 1978 *Scolecocoprns cameronensis* Brady; Decourten, p. 491, fig. 1A–C.
- 1987 *Taenidium cameronensis* (Brady); D'Alessandro and Bromley, p. 743, fig. 6.
- 1993 *Taenidium cameronensis* (Brady); Pickerill *et al.*, p. 63, fig. 2D.

*Diagnosis.* Unwalled meniscate burrows, secondary successive branching and intersection may be present. Meniscate packets usually longer than wide, with the deeply concave meniscate interfaces resulting in a nested appearance. (After D'Alessandro and Bromley 1987).

*Remarks.* This ichnotaxon was not clearly redefined by D'Alessandro and Bromley (1987). Although they retained the overall meaning of *Scolecocoprns* Brady, 1947, the accompanying illustration of the ichnotaxon by D'Alessandro and Bromley (1987, fig. 6) cannot be distinguished from the original illustration of *Scolecocoprns arizonensis* Brady, 1947. *S. arizonensis* has a different





TEXT-FIG. 6. *Taenidium barretti* (Bradshaw). Division of Natural Sciences, New Brunswick Museum, Saint John (NBMG); Grand Étang, Cape Breton Island, Nova Scotia, Canada; Pomquet Formation, middle Carboniferous; burrows from fluvio-lacustrine (shoreline) deposits. A i, ii, NBMG 9074; stereopair of full relief structures; thin-sectioning of the structures confirms that they are unwalled, the knobby outline being the result of irregular meniscate backpacking of sediment containing angular mudstone fragments;  $\times 0.7$ . B, NBMG 9217; top surface view of horizontally orientated (and inclined) specimens that have more uniform, silt-grade backfill, resulting in very indistinct menisci being preserved;  $\times 0.25$ . C, NBMG 9216; vertical section through slab, showing irregular meniscate structure that, in this case, indicates downward movement of producer;  $\times 1$ .

type of meniscate fill, approaching a chevron-shape, and is not synonymous with *Taenidium* because this ichnospecies contains a deeply grooved ornamentation at the base of the burrow. *T. cameronensis*, however, remains distinguishable from the similarly homogeneously backfilled *T. serpentinum* primarily by having packets longer than the burrow width.

*Taenidium barretti* (Bradshaw, 1981)

Plate 1; Text-figure 6

1968 'Scolicia' de Quatrafages; Webby, p. 1003, fig. 8.



- 1971 *Beaconites antarcticus* Vialov; Gevers *et al.*, p. 81, figs 1–2, 4.  
 1974 Problematica [= cf. *Beaconites antarcticus* Vialov; Pollard, 1976]; Ridgway, p. 511, fig. 1, pl. 17.  
 1975 *Beaconites* Vialov; Häntzschel, p. W45, fig. 28.1 [copy of Gevers *et al.*, 1971, fig. 2].  
 1981 *Beaconites antarcticus* Vialov; Allen and Williams, p. 255, figs 6–11.  
 \*1981 *Beaconites barretti* Bradshaw, p. 630, figs 17–18.  
 1981 *Scoyenia* isp.; Fürsich, p. 160, pl. 5 [*partim*].  
 1982 *Beaconites antarcticus* Vialov; Graham and Pollard, p. 259, figs 3A, 4A–C, 5A–B.  
 1982 Backfilled burrow; Nilsen, p. 79, fig. 46A.  
 ?1982 Meniscate burrow; Bown, p. 282, fig. 12B.  
 ?1982 Meniscate burrow; Bown and Kraus, p. 118, figs 7E–F, 8A–B.  
 1983 Horizontal feeding burrow; Maulik and Chaudhuri, p. 23, fig. 3.  
 1984 *Muensteria* isp.; Braken and Picard, p. 482, fig. 9.  
 1984 ?*Muensteria* isp.; Squires and Advocate, p. 594, figs 2A–F.  
 1985 cf. *Beaconites antarcticus* Vialov; Eagar *et al.*, p. 134, pl. 14A.  
 1985 Bivalve trace fossils; Thoms and Berg, p. 13, pl. 1C–E.  
 1986 Vertical burrows; Bridge *et al.*, p. 65, pl. 1b.  
 1987 *Beaconites barretti* Bradshaw; p. 259, figs 4–5.  
 1987 cf. *Ancorichnus coronus* Frey *et al.*; D'Alessandro *et al.*, p. 285, fig. 2.  
 1988 *Beaconites barretti* Bradshaw; Bradshaw and Webers, p. 787.  
 1990 *Beaconites* isp.; Dam and Andreasen, p. 208, fig. 11B.  
 1990 *Beaconites barretti* Bradshaw; Woolfe, p. 302, fig. 3.  
 1991 *Ancorichnus coronus* Frey *et al.*; Aceñolaza and Buatois, p. 96, pl. 2.1.  
 1991 Meniscate burrow; Diemer and Belt, p. 97, fig. 12 [*non Rhizocorallium*, p. 96].  
 1992 ?*Beaconites* Vialov; Pearson, p. 129, fig. 3D.  
 1992 *Beaconites barretti* Bradshaw; Tegan and Curran, p. A154.  
 1992 *Taenidium* Heer; Sarkar and Chaudhuri, p. 11, figs 4–5.  
 1993 *Taenidium* isp.; D'Alessandro *et al.*, p. 497, figs 3, 4B, 6B, 9, 10B [*partim*] 2, 6A, 10A, 12B.  
 1993 *Taenidium* Heer; Smith *et al.*, p. 590, fig. 14.  
 1993 *Ancorichnus coronus* Frey *et al.*; Aceñolaza and Buatois, p. 188, fig. 4D [copy of Aceñolaza and Buatois 1991, pl. 2.1].  
 1993 *Taenidium* isp.; Keighley and Pickerill, p. 83.  
 1993 *Taenidium barretti* (Bradshaw); Keighley and Pickerill, p. 83.

*Emended diagnosis.* Straight to variably meandering, unbranched, unwalled, meniscate backfilled burrow. Menisci are commonly hemispherical or deeply arcuate, tightly packed or stacked, forming non-compartmentalized backfill or thin meniscate segments.

*Remarks.* As previously discussed, menisci may merge laterally at the burrow boundary and in some preservational variants form a pseudo-wall or -lining. This is more likely where distinct segmentation of the backfill has been achieved. The boundary may be irregular to crenate, with individual meniscate segments slightly offset to one another (Graham and Pollard 1982). In full relief the burrow boundary may appear knobbly and similar to *Ophiomorpha irregulaire* Frey *et al.*, 1978 (Text-fig. 6A). The distinctiveness of menisci in the backfill is variable (Plate 1; Text-fig. 6B–C). Individual backfilled compartments may be so short in longitudinal section (thin segments) with respect to overall width, that distinct segmentation of the backfill is not achieved and the fill becomes irregular (non-compartmentalized). In addition, homogeneity in particle size or clast composition may result in the menisci being poorly defined when produced, and result in them being uniformly cemented and weathered. Many specimens from the Upper Palaeozoic are of giant size (up to 450 mm wide – Pearson 1992), although recorded widths (but not necessarily diameters – Graham and Pollard 1982) may be as small as 5 mm (Plate 1; Text-fig. 3). Almost all recordings are from non-marine environments (Text-fig. 5).

*T. barretti* is typically undulating and subparallel to stratification, although vertical sections, of similar diameter as the (sub-) horizontal burrow, may be dominant (e.g. Allen and Williams 1981a, Graham and Pollard 1982, Bracken and Picard 1984). Although previously interpreted as 'escape' or 'equilibrium' structures, some exclusively vertical 'burrows' are also included in the synonymy.

Simple downward displacement of primary sedimentary laminae is not an exclusive and distinguishing feature that can separate equilibrium structures from ichnospecies of repichnial *Taenidium*, that comprise arcuate non-faecal backfill (see Sarkar and Chaudhuri 1992, fig. 5).

### CONCLUSIONS

There is still a tendency for ichnologists to be influenced in naming a particular trace fossil depending on the interpreted depositional environment in which it is encountered. The classic example of this is the *Cruziana-Rusophycus* Hall, 1852 versus *Isopodichnus* Bornemann, 1899 debate, whereby several authors still persist in using the latter if a bilobate trace is encountered in non-marine rocks (see Bromley 1990). Similarly, the presence of large meniscate burrows in non-marine to marginal marine deposits appears to have automatically resulted in immediate comparison to *Beaconites* and, more recently, small lined backfilled structures to *Ancorichnus* without careful consideration of the significant criteria necessary for their nomenclature. *Ancorichnus* is unwalled but possesses a two zoned fill: an outer mantle with an internal, transverse to diagonal fabric, and an inner meniscate backfill. Simple meniscate structures with a distinct but unornamented and unstructured wall are considered to belong to *Beaconites*, whose ichnospecies are differentiated based on variations within the meniscate infill. *Taenidium* is a simple, unwalled, meniscate, backfilled structure, ichnospecies again being differentiated on the basis of variation within the meniscate infill (Text-fig. 2). We re-emphasize that depositional environment is not a valid diagnostic criterion, and workers should name their trace fossils solely on the basis of morphology. Without this directive, the development of workable ichnofacies/ichnocoenoses cannot be continued, since workers will be following the circular argument whereby a trace fossil is being utilized as an aid in the interpretation of a specific palaeoenvironment, but that palaeoenvironment is being inferred in the first place to name the trace fossil.

*Acknowledgements.* We thank R. MacNaughton and G. Narbonne for valuable discussion, C. Stanley for considered reviews of several versions of this manuscript, and R. Bromley and C. Cleal for suggesting important modifications, C. Colborne, A. Gómez, R. McCulloch, A. Murphy, D. Pirie and D. Tabor for technical assistance, and J. Kraus for providing translations of German manuscripts. The work was funded by an NSERC Canada grant to R. K. P. and constitutes part of D. G. K.'s Ph.D thesis.

### REFERENCES

- ACEÑOLAZA, F. G. and BUATOIS, L. A. 1991. Trazas fosiles del Paleozoico superior continental Argentino. *Ameghiniana*, **28**, 89–108.
- 1993. Nonmarine perigondwanic trace fossils from the late Paleozoic of Argentina. *Ichnos*, **2**, 183–203.
- ALEXANDRESCU, G. and BRUSTUR, T. 1978. Asupra unor urme de activitate organică (trace fossils) din fișul Carpaților orientali (Partea I). *Dări de Seamă ale Sedintelor. Institut de Geologie si Geofizică*, **65**, 17–30.
- ALLEN, J. R. L. 1961. Sandstone-plugged pipes in the Lower Old Red Sandstone of Shropshire, England. *Journal of Sedimentary Petrology*, **31**, 325–335.
- 1963. Depositional features of Dittonian rocks: Pembrokeshire, compared with the Welsh Borderland. *Geological Magazine*, **100**, 385–400.
- 1978. Locality B15 – Gelliswick Bay, Dyfed, 87–88. In FRIEND, P. F. and WILLIAMS, B. P. J. (eds). *A field guide to selected outcrop areas of the Devonian of Scotland, the Welsh Borderland, and South Wales*. Palaeontological Association, London, 106 pp.
- 1979. Old Red Sandstone facies in external basins, with particular reference to southern Britain. 65–80. In HOUSE, M. R., SCRUTTON, C. T. and BASSETT, M. G. (eds). *The Devonian System. Special Papers in Palaeontology*, **23**, 1–353.
- and WILLIAMS, B. P. J. 1978. The sequence of the earlier Lower Old Red Sandstone (Siluro-Devonian), north of Milford Haven, southwest Dyfed (Wales). *Geological Journal*, **13**, 113–136.
- 1981a. *Beaconites antarcticus*: a giant channel-dwelling trace fossil from the Lower Old Red Sandstone of South Wales and the Welsh Borders. *Geological Journal*, **16**, 255–269.

- ALLEN, J. R. L. and WILLIAMS, B. P. J. 1981*b*. Sedimentology and stratigraphy of the Townsend Tuff Bed (Lower Old Red Sandstone) in South Wales and the Welsh Borders. *Journal of the Geological Society, London*, **138**, 15–29.
- ARCHER, A. W. 1984. Preservational control of trace-fossil assemblages: Middle Mississippian carbonates of south-central Indiana. *Journal of Paleontology*, **58**, 285–297.
- BAMFORD, M. L., BRÜCK, P. M., COOPER, M. A., FORBES, W. H. and MACCARTHY, I. A. J. 1986. *Beaconites* – type burrows from the Old Red Sandstone of Hook Head, Co. Wexford, Ireland. *Proceedings of the Geologists' Association*, **97**, 59–71.
- BANDEL, K. 1973. A new name for the ichnogenus *Cylindrichmus* Bandel, 1967. *Journal of Paleontology*, **47**, 1002.
- BENTON, M. J. 1982. *Dictyodora* and associated trace fossils from the Palaeozoic of Thuringia. *Lethaia*, **15**, 115–132.
- BERG, T. M. 1977. Bivalve burrow structures in the Bellvale sandstone, New Jersey and New York. *Bulletin of the New Jersey Academy of Science*, **22**, 1–5.
- BJERSTEDT, T. W. 1988. Multivariate analyses of trace fossil distribution from an Early Mississippian oxygen-deficient basin, Central Appalachians. *Palaaios*, **3**, 53–68.
- BORNEMANN, J. G. 1899. Über den Buntsandstein in Deutschland seine Bedeutung für die Trias. *Beiträge zur Geologie und Paläontologie*, **1**, 1–61.
- BOWN, T. M. 1982. Ichnofossils and rhizoliths of the nearshore fluvial Jebel Qatrani Formation (Oligocene), Fayum Province, Egypt. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **40**, 255–309.
- and KRAUS, M. J. 1983. Ichnofossils of the alluvial Willwood Formation (Lower Eocene), Bighorn Basin, Northwest Wyoming, U.S.A. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **43**, 95–128.
- BRACKEN, B. and PICARD, M. D. 1984. Trace fossils from Cretaceous/Tertiary North Horn Formation in central Utah. *Journal of Paleontology*, **58**, 477–487.
- BRADSHAW, M. A. 1981. Palaeoenvironmental interpretations and systematics of Devonian trace fossils from the Taylor Group (Lower Beacon Supergroup), Antarctica. *New Zealand Journal of Geology and Geophysics*, **24**, 615–652.
- and WEBERS, G. F. 1988. The Devonian rocks of Antarctica. 783–795. In McMILLAN, N. J., EMBRY, A. F. and GLASS, D. J. (eds). *Devonian of the World. 1*. Proceedings of the Second International Symposium on the Devonian System, Calgary. Canadian Society of Petroleum Geologists, 795 pp.
- BRADY, L. F. 1947. Invertebrate tracks from the Coconino Sandstone of northern Arizona. *Journal of Paleontology*, **21**, 466–472.
- BRENCHLEY, P. J., ROMANO, M. and GUTIÉRREZ-MARCO, J. C. 1986. Proximal and distal hummocky cross-stratified facies on a wide Ordovician shelf in Iberia. 241–255. In KNIGHT, R. J. and McCLEAN, J. R. (eds). Shelf sands and sandstones. *Memoirs of the Canadian Society of Petroleum Geologists*, **11**, 1–347.
- BRIDGE, J. S. and DROSER, M. L. 1985. Unusual marginal-marine lithofacies from the Upper Devonian Catskill clastic Wedge. 143–161. In WOODROW, O. L. and SEVON, W. D. (eds). The Catskill Delta. *Geological Society of America, Special Paper*, **201**, 1–246.
- and GORDON, E. A. 1985. Quantitative interpretation of ancient river systems in the Oneonta Formation, Catskill Magnafacies. 168–181. In WOODROW, O. L. and SEVON, W. D. (eds). The Catskill Delta. *Geological Society of America, Special Paper*, **201**, 1–246.
- and TITUS, R. C. 1986. Non-marine bivalves and associated burrows in the Catskill Magnafacies, New York State. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **55**, 65–77.
- and NICKELSEN, B. H. 1985. Reanalysis of the Twilight Park Conglomerate, Upper Devonian Catskill Magnafacies, New York State. *Northeastern Geology*, **7**, 181–191.
- VAN VEEN, P. M. and MATTEN, L. C. 1980. Aspects of the sedimentology, palynology, and palaeobotany of the Upper Devonian of Southern Kerry Head, Co. Kerry, Ireland. *Geological Journal*, **15**, 143–170.
- BROMLEY, R. G. 1990. Trace fossils: biology and taphonomy. *Special Topics in Palaeontology*, **3**, 1–280.
- BRÜCK, P. M. 1987. A note on the trace fossil *Beaconites barretti* in the Old Red Sandstone of Co. Dublin, Ireland. *Proceedings of the Geologists' Association*, **98**, 259–263.
- FORBES, W. H., NANCE, D. and PICKERILL, R. K. 1985. *Beaconites antarcticus* in the (?middle) Late Devonian McAras Brook Formation, Cape George, Nova Scotia. *Maritime Sediments and Atlantic Geology*, **21**, 87–96.
- BURTON, B. R. and LINK, P. K. 1991. Ichnology of fine-grained mixed carbonate-siliclastic turbidites, Wood River Formation, Pennsylvanian-Permian, south-central Idaho. *Palaaios*, **6**, 291–301.
- CAREY, J. 1978. Sedimentary environments and trace fossils of the Permian Snapper Point Formation, southern Sydney basin. *Journal of the Geological Society of Australia*, **25**, 433–458.
- CHAMBERLAIN, C. K. 1971*a*. Morphology and ethology of trace fossils from the Ouachita Mountains, southeast Oklahoma. *Journal of Paleontology*, **45**, 212–246.



- 1971*b*. Bathymetry and paleoecology of Ouachita Geosyncline of southeastern Oklahoma as determined from trace fossils. *Bulletin of the American Association of Petroleum Geologists*, **55**, 34–50.
- 1975. Trace fossils in DSDP cores of the Pacific. *Journal of Paleontology*, **49**, 1074–1096.
- 1977. Ordovician and Devonian trace fossils from Nevada. *Bulletin of the Nevada Bureau of Mines and Geology*, **90**, 1–24.
- 1978*a*. Recognition of trace fossils in cores. 119–166. In BASAN, P. B. (ed.). Trace fossil concepts. *Society of Economic Paleontologists and Mineralogists, Short Course*, **5**, 1–181.
- 1978*b*. *A guidebook to the trace fossils and paleoecology of the Ouachita geosyncline*. Society of Economic Paleontologists and Mineralogists, 68 pp.
- 1979. Trace-fossil biofacies in the Lower and Middle Paleozoic of central Nevada. *Brigham Young University, Geology Studies*, **26**, 9–19.
- CLIFTON, H. E. and THOMPSON, J. K. 1978. *Macaronichnus segregatis*: a feeding structure of shallow marine polychaetes. *Journal of Sedimentary Petrology*, **48**, 1293–1302.
- CRIMES, T. P., GARCIA HIDALGO, J. F. and POIRE, D. G. 1992. Trace fossils from Arenig flysch sediments of Eire and their bearing on the early colonisation of the deep seas. *Ichnos*, **2**, 61–77.
- D'ALESSANDRO, A. and BROMLEY, R. G. 1987. Meniscate trace fossils and the *Muensteria*–*Taenidium* problem. *Palaeontology*, **30**, 743–763.
- EKDAL, A. A. and SONNINO, M. 1986. Sedimentologic significance of turbidite ichnofacies in the Saraceno Formation (Eocene), southern Italy. *Journal of Sedimentary Petrology*, **56**, 294–306.
- — — and PICARD, M. D. 1987. Trace fossils in fluvial deposits of the Duchesne River Formation (Eocene), Uinta Basin, Utah. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **61**, 285–301.
- LOICANO, F. and BROMLEY, R. G. 1993. Marine and nonmarine trace fossils and plant roots in a regressional setting (Pleistocene, Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, **98**, 495–522.
- DALEY, B. 1968. Sedimentary structures from a non-marine horizon in the Bembridge Marls (Oligocene) of the Isle of Wight, Hampshire, England. *Journal of Sedimentary Petrology*, **38**, 114–127.
- DAM, G. 1990*a*. Taxonomy of trace fossils from the shallow marine Lower Jurassic Neill Klintor Formation, East Greenland. *Bulletin of the Geological Society of Denmark*, **38**, 119–144.
- 1990*b*. Palaeoenvironmental significance of trace fossils from the shallow marine Lower Jurassic Neill Klintor Formation, East Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **79**, 221–248.
- and ANDREASEN, F. 1990. High-energy ephemeral stream deltas; an example from the Upper Silurian Holmestrand Formation of the Oslo Region, Norway. *Sedimentary Geology*, **66**, 197–225.
- DECOURTEN, F. L. 1978. *Scolecocoprus cameronensis* Brady (1947) from the Kaibab Limestone of the Northern Arizona: a reinterpretation. *Journal of Paleontology*, **52**, 491–493.
- DIEMER, J. A. and BELT, E. S. 1991. Sedimentology and paleohydraulics of the meandering river systems of the Fort Union Formation, southeastern Montana. *Sedimentary Geology*, **75**, 85–108.
- DINELEY, D. L. 1966. The Dartmouth Beds of Bigbury Bay, South Devon. *Journal of the Geological Society, London*, **122**, 187–217.
- DIXON, E. E. L. 1921. Geology of the South Wales coalfield, Part XIII. The country around Pembroke and Tenby. *Memoirs of the Geological Survey of Great Britain*, 1–220.
- EAGAR, R. M. C., BAINES, J. G., COLLINSON, J. D., HARDY, P. G., OKOLO, S. A. and POLLARD, J. E. 1985. Trace fossil assemblages and their occurrence in Silesian (mid-Carboniferous) deltaic sediments of the central Pennine Basin, England, 99–149. In CURRAN, H. A. (ed.). Biogenic structures: their use in interpreting depositional environments. *Special Publications, Society of Economic Paleontologists and Mineralogists*, **35**, 1–347.
- EDWARDS, P. 1975. Invertebrate burrows in an Oligocene fresh-water limestone. *Contributions to Geology*, **14**, 7–8.
- EKDAL, A. A. and PICARD, M. D. 1985. Trace fossils in a Jurassic eolianite, Entrada Sandstone, Utah, U.S.A. 3–12. In CURRAN, H. A. (ed.). Biogenic structures: their use in interpreting depositional environments. *Special Publications Society of Economic Paleontologists and Mineralogists*, **35**, 1–347.
- and BROMLEY, R. G. 1991. Analysis of composite ichnofabrics: an example in uppermost Cretaceous chalk of Denmark. *Palaeis*, **6**, 232–249.
- ÉKES, C. 1993. Bedload-transported pedogenic mud aggregates in the Lower Old Red Sandstone in southwest Wales. *Journal of the Geological Society, London*, **150**, 469–471.
- FISCHER-OOSTER, C. 1858, *Die fossilen Fucoiden der Schweizer-Alpen, nebst Erörterungen über deren geologisches Alter*. Huber, Bern, 72 pp.
- FORSYTH, I. H. and CHISHOLM, J. I. 1977. The geology of East Fifc. *Memoirs of the Geological Survey of Great Britain*, 1–284.

- FREY, R. N. 1990. Trace fossils and hummocky cross-stratification, Upper Cretaceous of Utah. *Palaos*, **5**, 203–218.
- and HOWARD, J. D. 1970. Comparison of Upper Cretaceous ichnofaunas from siliceous sandstones and chalk, Western Interior Region, U.S.A. 141–166. In CRIMES, T. P. and HARPER, J. C. (eds). Trace fossils. *Geological Journal, Special Issue*, **3**, 1–547.
- 1982. Trace fossils from the Upper Cretaceous of the Western Interior. *Mountain Geologist*, **19**, 1–10.
- 1985a. Trace fossils from the Panther member, Star Point Formation (Upper Cretaceous), Coal Creek Canyon, Utah. *Journal of Paleontology*, **59**, 370–404.
- 1985b. Upper Cretaceous trace fossils, Book Cliffs of Utah: a field guide. 115–152. In KAMOLA, D. L., PFAFF, B. J., NEWMAN, S. L., FREY, R. N. and HOWARD, J. D. (eds). Depositional facies of the Castlegate and Blackhawk Formations, Book Cliffs, eastern Utah. *Society of Economic Paleontologists and Mineralogists midyear meeting, Golden, Colorado, Field Trip 10*, 152 pp.
- 1990. Trace fossils and depositional sequences in a clastic shelf setting, Upper Cretaceous of Utah. *Journal of Paleontology*, **64**, 803–820.
- and PRYOR, W. A. 1984. *Ophiomorpha*: its morphologic, taxonomic and environmental significance. *Palaogeography, Palaeoclimatology, Palaeoecology*, **23**, 199–229.
- and PEMBERTON, S. G. 1985. Biogenic structures in outcrops and cores. I. Approaches to ichnology. *Bulletin of the Canadian Society of Petroleum Geologists*, **33**, 72–115.
- and FAGERSTROM, J. A. 1984. Morphological, ethological and environmental significance of the ichnogenera *Scoyenia* and *Ancorichnus*. *Journal of Paleontology*, **58**, 511–518.
- FÜRSICH, F. T. 1974. Corallian (Upper Jurassic) trace fossils from England and Normandy. *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)*, **13**, 1–52.
- 1981. Invertebrate trace fossils from the Upper Jurassic of Portugal. *Comunicações dos Geólogos de Portugal*, **67**, 153–168.
- and HEINBERG, C. 1983. Sedimentology, biostratigraphy, and palaeoecology of an Upper Jurassic offshore sand bar complex. *Bulletin of the Geological Society of Denmark*, **32**, 67–95.
- GAILLARD, C. 1980. *Megagyrolithes ardescensis* n. gen. n. sp. trace fossile nouvelle du Valanginian d'Ardeche (France). *Geobios*, **13**, 465–471.
- GERMS, G. J. B. 1972. Trace fossils from the Nama Group, South-west Africa. *Journal of Paleontology*, **46**, 864–870.
- GEVERS, J. W., FRANKS, L. A., EDWARDS, L. N. and MARZOLF, J. E. 1971. Trace fossils in the Lower Beacon Sediments (Devonian) Darwin Mountains, Southern Victoria Land, Antarctica. *Journal of Paleontology*, **45**, 81–94.
- and TWOMEY, A. 1982. Trace fossils and their environment in Devonian (Silurian?) Lower Beacon strata in the Asgard Range, Victoria Land, Antarctica. 639–649. In CRADDOCK, C. (ed.). *Antarctic geoscience*. International Union of Geological Sciences, University of Wisconsin Press, Madison, 1172 pp.
- GIERLOWSKI-KORDESCH, E. 1991. Ichnology of an ephemeral lacustrine/alluvial plain system: Jurassic East Berlin Formation, Hartford Basin, USA. *Ichnos*, **1**, 221–232.
- GLOCKER, E. F. 1841. Über eine neue räthelhafte Versteinerung aus dem thonigen Sphärosiderit der Karpathensandsteinformation im Gebiete der Beskiden, nebst vorangeschickten Bemerkungen über die Versteiner dieses Gebietes überhaupt. *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum*, **19**, 675–700.
- GÖPPERT, H. R. 1841. Über die fossile Flora der Quadersandsteinformation in Schlesien als erster Beitrag zur Flora der Tertiärgebilde. *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum*, **19**, 97–134.
- GORDON, E. A. 1988. Body and trace fossils from the middle-upper Devonian Catskill Magnafacies, southeastern New York, U.S.A. 139–155. In McMILLAN, N. J., EMBRY, A. F. and GLASS, D. J. (eds). *Devonian of the World. Vol. II*. Proceedings of the 2nd International Symposium on the Devonian System, Calgary. Canadian Society of Petroleum Geologists, 679 pp.
- GRAHAM, J. R. and POLLARD, J. E. 1982. Occurrence of the trace fossil *Beaconites antarcticus* in the Lower Carboniferous fluvial rocks of County Mayo, Ireland. *Palaogeography, Palaeoclimatology, Palaeoecology*, **38**, 257–268.
- GÜMBEL, C. W. 1879. *Geognostische Beschreibung des Fichtelgebirges mit dem Frankenwalde und dem westlichen Vorlande* 3. Perthes, Gotha, 698 pp.
- HÄNTZSCHEL, W. 1962. Trace fossils and problematica. 178–245. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology, Part W. Miscellaneous*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 259 pp.

- 1972. Lebensspuren in den Kulm-Tonschiefern von Neustadt a.d. Weinstrasse. *Oberrheinische geologische Abhandlungen*, **21**, 107–115.
- 1975. Trace fossils and problematica. 1–269. In TEICHERT, C. (ed.). *Treatise on invertebrate paleontology, Part W. Miscellanea, Supplement 1*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 269 pp.
- HAKES, W. G. 1976. Trace fossils and depositional environments of four clastic units, Upper Pennsylvanian megacyclothems, northeast Kansas. *University of Kansas Paleontological Contributions*, **63**, 1–46.
- 1985. Trace fossils from brackish-marine shales, Upper Pennsylvanian of Kansas, U.S.A. 21–35. In CURRAN, H. A. (ed.). Biogenic structures: their use in interpreting depositional environments. *Special Publication, Society of Economic Paleontologists and Mineralogists*, **35**, 1–347.
- HALL, J. 1852. *Palaeontology of New York, Volume 2*. State of New York, Albany, 362 pp.
- HALLAM, A. 1960. *Kulindrichinus langi*, a new trace fossil from the Lias. *Palaeontology*, **3**, 64–68.
- HASKELL, T. C., KENNETT, J. P. and PREBBLE, W. M. 1965. Geology of the Brown Hills and Darwin Mountains, Southern Victoria Land, Antarctica. *Transactions of the Royal Society of New Zealand*, **2**, 231–248.
- HEER, O. 1865. *Die Urwelt der Schweiz*. F. Schulthess, Zurich, 622 pp.
- 1877. *Flora fossilis Helvetiae. Die vorweltliche Flora der Schweiz*. J. Würster and Co., 182 pp.
- 1881. *Contributions à la flore fossile due Portugal. (Section des Travaux géologiques du Portugal)*. Lisbon, 51 pp.
- HEINBERG, C. 1970. Some Jurassic trace fossils from Jameson Land (East Greenland). 227–234. In CRIMES, T. P. and HARPER, J. C. (eds). Trace fossils. *Geological Journal Special Issue*, **3**, 1–347.
- 1974. A dynamic model for a meniscus filled tunnel (*Ancorichnus* n. ichnogen.) from the Jurassic Pecten Sandstone of Milne Land, East Greenland. *Rapport Gronlands Geologiske Undersogelse*, **62**, 1–20.
- and BIRKELUND, T. 1984. Trace fossil assemblages and basin evolution of the Vardekløft Formation (Middle Jurassic, central East Greenland). *Journal of Paleontology*, **58**, 362–387.
- HORNE, R. R. and GARDINER, P. R. R. 1973. A new trace fossil from non-marine Upper Palaeozoic red beds in County Wexford and County Kerry, Ireland. *Geologie en Mijbouw*, **52**, 125–131.
- HOSIUS, A. and VON DER MARCK, W. 1880. Die Flora der Westfälischen Kreideformation. *Palaeontographica*, **26**, 125–236.
- HOWARD, J. D. 1966. Characteristic trace fossils in Upper Cretaceous sandstones of the Book Cliffs and Wasatch Plateau. *Bulletin, Utah Geological and Mineralogical Survey*, **80**, 35–53.
- 1971. Comparison of the beach to offshore sequence in modern and ancient sediments. 149–183. In HOWARD, J. D., VALENTINE, J. W. and WARME, J. E. (eds). *Recent advances in paleoecology and ichnology. Short course*. American Geological Institute, 268 pp.
- 1972. Trace fossils as criteria for recognising shorelines in the stratigraphical record. 215–225. In RIGBY, J. K. and HAMBLIN, W. K. (eds). Recognition of ancient sedimentary environments. *Special Publication, Society of Economic Paleontologists and Mineralogists*, **16**, 1–340.
- and FREY, R. W. 1984. Characteristic trace fossils in nearshore to offshore sequences, Upper Cretaceous of east-central Utah. *Canadian Journal of Earth Sciences*, **21**, 200–219.
- KEIGHLEY, D. G. and PICKERILL, R. K. 1993. Nonmarine invertebrate ichnocoenoses from the Carboniferous of Cape Breton Island. (Abstract). *Atlantic Geology*, **29**, 83.
- KERN, J. P. 1978. Trails from the Vienna woods: paleoenvironments and trace fossils of Cretaceous to Eocene flysch, Vienna, Austria. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **23**, 231–262.
- KSIĄŻKIEWICZ, M. 1977. Trace fossils in the flysch of the Polish Carpathians. *Palaeontologia Polonica*, **36**, 1–208.
- LESSERTISSEUR, J. 1955. Traces fossiles d'activité animale et leur signification paléobiologique. *Mémoires de la Société Géologique de France*, **74**, 1–48.
- LESZCZYNSKI, S. 1991. Trace-fossil tiering in flysch sediments: examples from the Guipúzcoan flysch (Cretaceous-Paleogene), northern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **88**, 167–184.
- LIBURNAU, J. R. R. L. VON 1990. Zur deutung der fossilen fucoiden-gattungen *Taenidium* und *Gyrophyllites*. *Denkschriften der Akademie der Wissenschaften Wien*, **70**, 523–583.
- LOCKLEY, M. G., RINDSBERG, A. K. and ZEILER, R. M. 1987. The paleoenvironmental significance of the nearshore *Curvolithus* ichnofacies. *Palaïos*, **2**, 255–262.
- MACDONALD, D. I. M. 1982. Palaeontology and ichnology of the Cumberland Bay Formation, South Georgia. *Bulletin, British Antarctic Survey*, **57**, 1–14.
- MACLEAY, W. S. 1839. Note on the annelida. 699–701. In MURCHISON, R. I. *The Silurian System*. J. Murray, London, 768 pp.
- MAILLARD, G. A. 1887. Considérations sur les fossiles décrits comme Algues. *Mémoires de la Société Paléontologique Suisse*, **14**, 1–40.



- MAPLES, C. G. and ARCHER, A. W. 1989. The potential of Paleozoic nonmarine trace fossils for paleoecological interpretations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **73**, 185–195.
- and SUTTNER, L. J. 1990. Trace fossils and marine-nonmarine cyclicality in the Fountain Formation (Pennsylvanian: Morrowan/Atokan) near Manitou Springs, Colorado. *Journal of Paleontology*, **64**, 859–880.
- MARTINO, R. L. 1989. Trace fossils from marginal marine facies of the Kanawha Formation (Middle Pennsylvanian), West Virginia. *Journal of Paleontology*, **63**, 389–403.
- MASSALONGO, A. 1855. *Zoophycos, novum genus plantorum fossilium*. Antonelli, Verona, 52 pp.
- MAULIK, P. K. and CHAUDHURI, A. K. 1983. Trace fossils from continental Triassic red beds of the Gondwana sequence, Pranhita-Godavari valley, South India. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **41**, 17–34.
- MCCANN, T. and PICKERILL, R. K. 1988. Flysch trace fossils from the Cretaceous Kodiak Formation of Alaska. *Journal of Paleontology*, **62**, 330–348.
- MCCARTHY, B. 1979. Trace fossils from a Permian shoreface-foreshore environment, eastern Australia. *Journal of Paleontology*, **53**, 345–366.
- McKELVEY, B. C., WEBB, P. N. and KOHN, B. P. 1977. Stratigraphy of the Taylor and Lower Victoria Groups (Beacon Supergroup) between the MacKay glacier and Boomerang ridge, Antarctica. *New Zealand Journal of Geology and Geophysics*, **20**, 813–863.
- MIKULÁS, R. 1990. Trace fossils from the Zahorany Formation (Upper Ordovician, Bohemia). *Acta Universitatis Carolinae, Geologica*, **3**, 307–335.
- 1992. Trace fossils from Early Silurian graptolitic shales of the Prague Basin (Czechoslovakia). *Casopis pro Mineralogii a Geologii*, **37**, 219–228.
- 1993. Trace fossils and ichnofacies of the Ordovician of the Prague Basin (central Bohemia, Czech Republic). *Boletín de la Real Sociedad Española de Historia Natural. Sección Geológica*, **88**, 99–112.
- MILLER, W. 1986. Discovery of trace fossils in Franciscan turbidites. *Geology*, **14**, 343–345.
- 1989. Paleontology of Franciscan Flysch at Point Saint George, Northern California. 47–52. In AALTO, K. R. and HARPER, G. D. (eds). *Geologic evolution of the northernmost Coast Ranges and western Klamath Mountains, California*. 28th International Geological Congress, Field Trip Guidebook T308, 82 pp.
- 1991a. Intrastratal trace fossil zonation, Cretaceous flysch of northern California. *Ichnos*, **1**, 161–171.
- 1991b. Bathysiphonid (Protista: Foraminiferida) localities in Franciscan flysch, Northern California, with a redescription of *Bathysiphon aaltoi* Miller, 1986. *Tulane Studies in Geology and Paleontology*, **24**, 71–78.
- MÜLLER, A. H. 1966. Neue Lebensspuren (Vestigia invertebratorum) aus dem Karbon und der Triasa Mitteldeutschlands. *Geologie*, **15**, 712–725.
- NARBONNE, G. M. 1984. Trace fossils in Upper Silurian tidal flat to basin slope carbonates of Arctic Canada. *Journal of Paleontology*, **58**, 398–415.
- and HOFMANN, H. J. 1987. Ediacaran biota of the Wernecke Mountains, Yukon, Canada. *Palaeontology*, **30**, 647–676.
- MYROW, P. M., LANDING, E. and ANDERSON, M. M. 1987. A candidate stratotype for the Precambrian-Cambrian boundary, Fortune Head, Burin Peninsula, southeastern Newfoundland. *Canadian Journal of Earth Sciences*, **24**, 1277–1293.
- NATHORST, A. G. 1880. Om spår af några evertbererade djur M.M. och deras paleontologiska betydelse. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, **18**, 1–104.
- NILSEN, T. H. 1982. Alluvial fan deposits. 49–86. In SCHOLLE, P. A. and SPEARING, D. (eds). Sandstone depositional environments. *Memoirs of the American Association of Petroleum Geologists*, **31**, 1–410.
- OOSTER, W. A. 1869. Die organischen Reste der *Zoophycos*-Schichten der Schweizer-Alpen. 3–35. In OOSTER, W. A. and FISCHER-OOSTER, C. (eds). *Protozoa Helvetica*. H. Georg, Basel and Zurich, 43 pp.
- ORBIGNY, A. D' 1842. *Voyage dans l'Amérique méridionale*. 3 (4) (*Paléontologie*). Levrault, Strasbourg, 188 pp.
- O'SULLIVAN, M. J., COOPER, M. A., MCCARTHY, I. A. J. and FORBES, W. H. 1986. The palaeoenvironment and deformation of a 'Beaconites' colony in the Old Red Sandstone at Gortnabrinna, southwest Ireland. *Journal of the Geological Society, London*, **143**, 897–906.
- PAPP, A. 1941. Quergegliederte Röhren aus dem Ober-Kriede-Flysch der Alpen. *Palaeobiologica*, **7**, 314–317.
- PEARSON, P. N. 1992. Walking traces of the giant myriapod *Arthropleura* from the Strathclyde Group (Lower Carboniferous) of Fife. *Scottish Journal of Geology*, **28**, 127–133.
- PEDERSEN, G. K. and SURLYK, F. 1983. The Fur Formation, a late Paleocene ash-bearing diatomite from northern Denmark. *Bulletin of the Geological Society of Denmark*, **32**, 43–65.

- PEMBERTON, S. G. and FREY, R. W. 1982. Trace fossil nomenclature and the *Planolites-Palaeophycus* dilemma. *Journal of Paleontology*, **56**, 843–881.
- 1984. Ichnology of storm-influenced shallow marine sequence: Cardium Formation (Upper Cretaceous) at Seebe, Alberta. 281–304. In STOTT, D. F. and GLASS, D. J. (eds). *The Mesozoic of Middle North America. Memoirs of the Canadian Society of Petroleum Geologists*, **9**, 1–573.
- and BROMLEY, R. G. 1988. The ichnotaxonomy of *Conostichus* and other plug-shaped ichnofossils. *Canadian Journal of Earth Sciences*, **25**, 866–892.
- PERKINS, B. F. and STEWART, C. L. 1971. Preface to stops 7 through 12. 56–70. In PERKINS, B. F. (ed.). *A field guide to selected localities in Pennsylvanian, Permian, Cretaceous, and Tertiary rocks of Texas and related papers*. Society of Economic Paleontologists and Mineralogists Field Trip Guidebook April 1971, 148 pp.
- PFEIFFER, H. 1966. Die spurenfossilien des Kulms (Dinanats) und Devons der Frankenwälder Querzone (Thüringen). *Jahrbuch für Geologie*, **2**, 651–717.
- PICKERILL, R. K. 1980. Phanerozoic flysch trace fossil diversity – observations based on an Ordovician flysch ichnofauna from the Aroostook-Matapedia Carbonate Belt of northern New Brunswick. *Canadian Journal of Earth Sciences*, **17**, 1259–1270.
- 1989. *Compaginaticnus*: a new ichnogenus from Ordovician flysch of eastern Canada. *Journal of Paleontology*, **63**, 913–919.
- 1994. Nomenclature and taxonomy of invertebrate trace fossils. 3–42. In DONOVAN, S. K. (ed.). *The palaeobiology of trace fossils*. John Wiley and Sons, Chichester, 306 pp.
- DONOVAN, S. K., DOYLE, E. N. and DIXON, H. L. 1993. Ichnology of the Palaeogene Richmond Formation of eastern Jamaica – the final chapter? *Atlantic Geology*, **29**, 61–67.
- FYFFE, L. R. and FORBES, W. H. 1987. Late Ordovician–Early Silurian trace fossils from the Matapedia Group, Tobique River, western New Brunswick, Canada. *Maritime Sediments and Atlantic Geology*, **23**, 77–88.
- and HARLAND, T. L. 1988. Trace fossils from Silurian slope deposits, North Greenland. *Rapport Gronlands Geologiske Undersogelse*, **137**, 119–133.
- ROMANO, M. and MELÉNDEZ, B. 1984. Arenig trace fossils from the Salamanca area, western Spain. *Geological Journal*, **19**, 249–269.
- PIENKOWSKI, G. 1985. Early Liassic trace fossil assemblages from the Holy Cross Mountains, Poland: their distribution in continental and marginal marine environments. 37–51. In CURRAN, H. A. (ed.). *Biogenic structures: their use in interpreting depositional environments. Special Publication, Society of Economic Paleontologists and Mineralogists*, **35**, 1–347.
- PLUME, R. W. 1983. Environmental interpretation of the New Mountain Subgroup – marine or non-marine (Beacon Supergroup). (Abstract). 233. In OLIVER, R. L., JAMES, P. R. and JAGO, J. B. (eds). *Antarctic Earth science*. Cambridge University Press, Cambridge, 697 pp.
- POLLARD, J. E. 1976. A problematical trace fossil from the Tor Bay Breccias of South Devon. *Proceedings of the Geologists' Association*, **87**, 105–108.
- 1988. Trace fossils in coal-bearing sequences. *Journal of the Geological Society, London*, **145**, 339–350.
- STEEL, R. J. and UNDERSUND, E. 1982. Facies sequences and trace fossils in lacustrine/fan delta deposits, Hornelen Basin, (Middle Devonian), western Norway. *Sedimentary Geology* **32**, 63–87.
- POWICHOŃSKI, L. K. 1989. Trace fossils from the Helminthoid Flysch (Upper Cretaceous–Paleocene) of the Ligurian Alps (Italy): development of deep marine ichnoassociations in fan and basin plain environments. *Eclogae Geologicae Helvetiae*, **82**, 385–411.
- QUATREFAGES, M. A. DE 1849. Note sur la *Scolicia prisca* (A. de Q.), annélide fossile de la craie. *Annales des Sciences Naturelles, Série 3*, **12**, 265–266.
- RIDGWAY, J. M. 1974. A problematical trace fossil from the New Red Sandstone of South Devon. *Proceedings of the Geologists' Association*, **85**, 511–517.
- RINDSBERG, A. K. 1990. Commentary: ichnological consequences of the 1985 International Code of Zoological Nomenclature. *Ichnos*, **1**, 59–63.
- ROMANO, M. 1991. Lower to Middle Ordovician trace fossils from the Central Iberian Zone of Portugal and Spain. 191–204. In BARNES, C. R. and WILLIAMS, S. H. (eds). *Advances in Ordovician geology. Papers, Geological Survey of Canada*, **90-9**, 326 pp.
- SACCO, F. 1888. Note di paleoicnologia Italiana. *Afti della Società Italiana di Scienze Naturali*, **31**, 151–191.
- SARKAR, S. and CHAUDHURI, A. K. 1992. Trace fossils in Middle to Late Triassic fluvial redbeds, Pranhita-Godavari Valley, South India. *Ichnos*, **2**, 7–19.
- SCHÄFER, W. 1956. Wirkungen der Benthos-Organismen auf der jungen Schichtverband. *Senckenbergiana Lethaea*, **37**, 183–263.

- SCHAFHÄUTL, K. E. 1851. *Geognostische Untersuchung des südbayerischen Alpengebirges*. Literarischen-artische Anstalt, Munich, 208 pp.
- SCASSO, R. A., OLIVERO, E. B. and BUATOIS, L. A. 1991. Lithofacies, biofacies and ichnoassemblage evolution of a shallow submarine volcanoclastic fan-shelf depositional system (Upper Cretaceous), James Ross Island, Antarctica. *Journal of South American Earth Sciences*, **4**, 239–260.
- SCHIMPER, W. P. 1869. *Traité de Paléontologie végétale*. J. B. Baillière et fils, Paris, 740 pp.
- and SCHENK, A. 1890. Palaeophytologie. 44–68, 233–234. In ZITTEL, K. A. (ed). *Handbuch Paläontologie*. Oldenbourg, Munich and Leipzig, 958 pp.
- SCHRÖTER, 1894. Notiz über ein *Taenidium* aus dem Flysch von Ganey bei Seewis. *Jahresbericht der Naturforschenden Gesellschaft Graubündens Chur*, **37**, 79–87.
- SCOTT, A. C., EDWARDS, D. and ROLFE, W. D. I. 1976. Fossiliferous Lower Old Red Sandstone near Cardross, Dumbartonshire. *Proceedings of the Geological Society of Glasgow*, **117**, 4–5.
- SEILACHER, A. 1955. Spuren und Fazies im Unterkambrium. 373–399. In SCHINDEWOLF, O. H. and SEILACHER, A. (eds). Beiträge zur Kenntnis des Kambriums in der Salt Range (Pakistan). *Abhandlung der Mathematisch-naturwissenschaftlichen Klasse. Akademie der Wissenschaften und der Literatur, Mainz*, **10**, 1–796.
- 1958. Flysch und Molasse als Faziestypen. *Eclogae Geologicae Helveticae*, **51**, 1062–1078.
- 1962. Paleontological studies on turbidite sedimentation and erosion. *Journal of Geology*, **70**, 227–234.
- 1964. Biogenic sedimentary structures. 296–316. In IMBRIE, J. and NEWELL, N. (eds). *Approaches to paleoecology*. Wiley, New York, 432 pp.
- 1978. Use of trace-fossil assemblages for recognizing depositional environments. 167–181. In BASAN, P. B. (ed.). *Trace fossil concepts. Short Course No. 5*. Society of Economic Paleontologists and Mineralogists, 181 pp.
- SMITH, R. M. H., MASON, T. R. and WARD, J. D. 1993. Flash-flood sediments and ichnofacies of the Late Pleistocene Homeb Silts, Kuiseb River, Namibia. *Sedimentary Geology*, **85**, 579–599.
- SQUINABOL, S. 1887. Contribuzioni alla flora fossile dei terreni Terziarii della Liguria. *Bollettino della Società Geologica Italiana*, **6**, 545–561.
- 1891. *Contribuzioni alla flora fossile dei terreni Terziarii della Liguria. I. Algae*. Genova. 25 pp.
- SQUIRES, R. L. and ADVOCATE, D. M. 1984. Meniscate burrows from Miocene lacustrine-fluvial deposits, Diligencia Formation, Orocochia Mountains, southern California. *Journal of Paleontology*, **58**, 593–597.
- STANISTREET, I. G., LE BLANC SMITH, G. and CADLE, A. B. 1980. Trace fossils as sedimentological and palaeoenvironmental indices in the Ecca Group (Lower Permian) of the Transvaal. *Transactions of the Geological Society of South Africa*, **83**, 333–344.
- STANLEY, D. C. A. and PICKERILL, R. K. 1993. *Fustiglyphus annulatus* from the Ordovician of Ontario, Canada, with a systematic review of the ichnogenera *Fustiglyphus* Vialov 1971 and *Rhabdoglyphus* Vassioevich 1951. *Ichnos*, **3**, 57–67.
- STANLEY, K. O., CHAMBERLAIN, C. K. and STEWART, J. H. 1977. Depositional setting of some eugeosynclinal Ordovician rocks and structurally interleaved Devonian rocks in the Cordilleran mobile belt, Nevada. 259–274. In STEWART, J. H., STEVENS, C. H. and FRITSCH, A. E. (eds). *Paleozoic paleogeography of the western United States. Pacific Coast Paleogeography Symposium, 1. April 1977*. Society of Economic Paleontologists and Mineralogists, 502 pp.
- and FAGERSTROM, J. A. 1974. Miocene invertebrate trace fossils from a braided river environment, Western Nebraska, U.S.A. *Paleogeography, Palaeoclimatology, Palaeoecology*, **15**, 63–82.
- STERNBERG, K. M. VON 1833. *Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt*, 5–6. Fleischer Fr., Leipzig, Prague, 80 pp.
- TEGAN, J. R. and CURRAN, H. A. 1992. Response of infaunal organisms represented by trace fossils to sea-level changes in the Ordovician Black River and Trenton Group limestones, upstate New York (Abstract). A154. *Geological Society of America Abstracts and Program, 1992 Annual Meeting*. Cincinnati, 365 pp.
- TEVESZ, M. J. S. and MCCALL, P. L. 1982. Geological significance of aquatic nonmarine trace fossils. 257–285. In MCCALL, P. L. and TEVESZ, M. J. S. (eds). *Animal-sediment relations*. Plenum, New York, 336 pp.
- THOMS, R. E. and BERG, T. H. 1985. Interpretation of bivalve trace fossils in fluvial beds of the basal Catskill Formation (Late Devonian), Eastern USA. 13–20. In CURRAN, H. A. (ed.). *Biogenic structures: their use in interpreting depositional environments. Special Publication, Society of Economic Paleontologists and Mineralogists*, **35**, 1–347.
- TOOTS, H. 1967. Invertebrate burrows in the non-marine Miocene of Wyoming. *Contributions to Geology University of Wyoming*, **6**, 93–96.
- TREWIN, N. H. 1976. *Isopodichnus* in a trace fossil assemblage from the Old Red Sandstone. *Lethaia*, **9**, 29–37.



- VALENZUELA, M., GARCIA-RAMOS, J. C. and SUAREZ DE CENTI, C. 1986. The Jurassic sedimentation in Asturias (N. Spain). *Trabajos de Geologia*, **16**, 121–132.
- VASSOIEVICH, N. B. 1951. *Usloviya obrazovaniya flisha*. Gostoptekhizdat, Leningrad and Moscow, 240 pp.
- VIALOV, O. S. 1962. Problematica of the Beacon Sandstone at Beacon Heights, West Antarctica. *New Zealand Journal of Geology and Geophysics*, **5**, 718–732.
- 1971. Redkie problematiki iz mezozoya Pamira i Kaukaza. *Paleontologicheskii Sbornik*, **7**, 85–93.
- WALCOTT, C. D. 1890. The fauna of the Lower Cambrian or Olenellus Zone. *Report of the United States Geological Survey*, **10**, 515–760.
- WALTER, M. R., ELPHINSTONE, R. and HEYS, G. R. 1989. Proterozoic and Early Cambrian trace fossils from the Amadeus and Georgina Basins, central Australia. *Alcheringa*, **13**, 209–256.
- WEBBY, B. P. 1968. Devonian trace fossils from the Beacon Group of Antarctica. *New Zealand Journal of Geology and Geophysics*, **11**, 1001–1008.
- WETZEL, A. 1983. Biogenic structures in modern slope to deep-sea sediments in the Sulu Sea Basin (Philippines). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **42**, 285–304.
- WHEATCROFT, R. 1986. Maestrichtian trace fossils from selected localities in the Chattahoochee River valley, 57–70. In REINHARDT, J. (ed.). *Stratigraphy and sedimentology of continental, nearshore, and marine Cretaceous sediments of the eastern Gulf coastal plain*. SEPM/AAPG annual meeting 1986. Field Trip 3, 99 pp.
- WHITE, C. D. 1929. Flora of the Hermit Shale, Grand Canyon, Arizona. *Publications, Carnegie Institution of Washington*, **405**, 1–221.
- WIEDMAN, L. A. and FELDMANN, R. M. 1988. Ichnofossils, tubiform body fossils, and depositional environment of the La Meseta Formation (Eocene) of Antarctica. *Memoirs, Geological Society of America*, **169**, 531–539.
- WILCKENS, O. 1947. Paläontologische und geologische Ergebnisse der Reise von Kohl-Larsen (1928–29) nach Süd-Georgien. *Abhandlungen der Seuchenbergischen Naturforschenden Gesellschaft*, **474**, 1–75.
- WILLIAMS, B. P. J. 1978. Locality B18 – Freshwater West, Dyfed. 95–98. In FRIEND, P. F. and WILLIAMS, B. P. J. (eds). *A field guide to selected outcrop areas of the Devonian of Scotland, the Welsh Borderland, and South Wales*. Palaeontological Association, London, 106 pp.
- WOOLFE, K. J. 1990. Trace fossils as paleoenvironmental indicators in the Taylor Group (Devonian) of Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **80**, 301–310.
- ZENKER, J. C. 1836. *Historisch-topographisches Taschenbuch von Jena und seiner Umgebung besonders in naturwissenschaftlicher und medicinischer Beziehung*. Wackenhoder, Jena, 338 pp.

D. G. KEIGHLEY

R. K. PICKERILL

Department of Geology  
University of New Brunswick  
Fredericton, Canada E3B 5A3

Typescript received 29 June 1993

Revised typescript received 27 January 1994